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ASCOMATAL DEVELOPMENT IN LICHENS: A REVIEW

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ABSTRACT - From some examples, four of which being studied with details, a comparative study of ascomatal development in Lichens has been attempted. Three fundamental stages are distinguished: primordium stage, "ébauche" stage, and stage with parathecial formations. The structural components of ascomata are analysed as well as the different growth modalities during the ontogenetical stages. The opening of the fruiting bodies and some peculiarities in the development are then studied. The different types of adult ascomata are compared and the main ontogenetical types of ascomata are succinctly described. The systematical value of ascoma development is, at last, briefly discussed.

RÉSUMÉ - A partir d'exemples, dont quatre sont étudiés en détail, on a tenté de faire une étude comparée du développement de l'ascoma chez les Lichens. Trois stades fondamentaux sont distingués (le stade primordium, le stade ébauche et le stade avec formations parathéciales). Les éléments structuraux des ascomata sont analysés ainsi que les modalités de croissance au cours des différents stades du développement. Après l'étude de l'ouverture des fructifications et de quelques particularités du développement, les différents types d'ascocarpes adultes sont comparés. Les principaux types ontogéniques d'ascomata sont ensuite sommairement décrits. La valeur systématique de l'étude du développement des ascomata est brièvement discutée.

Since a long time, authors who wished to clarify relations between Ascolichens, Ascomycetes and Algae, have studied morphology and ontogeny of ascomata : TULASNE (1852), KRABBE (1882, 1891), REINKE (1895), BAUR (1898, 1901, 1904), WOLFF (1905), NIENBURG (1908), MOREAU & MOREAU (1928). After years with no further interest, new researches started, first with DOPPELBAUR (1959 and 1960), then with LETROUIT-GALINOU (since 1960), HENSSEN (since 1963) and their students, specially JAHNS (since 1970), JANEX-FAVRE (since 1965), KEUCK (1977, 1979). Besides recent reviews on the subject by LETROUIT-GALINOU (1973), HENSSEN & JAHNS (1974), HENSSEN (1976, 1981), PARGUEY-LEDUC &

JANEX-FAVRE (1981), general considerations are also included in KEUCK (1977) and SIPMAN (1983) who attempt to harmonize concepts and to clarify terminology. Of peculiar interest are also the synthetic considerations developed recently by CHADEFAUD (1982 a,b,c), concerning ascomatal structure and evolution.

The present paper attempts to a comparative analysis of datas relative to structure and development of the sterile elements in lichen ascomata. Concerning the fertile elements (ascogonial apparatus, sporophytic apparatus, asci and ascospores), a review has been recently published (BELLEMERE & LETROUIT, 1988), so these will not be specially considered here.

Morphological and structural terminology will be first briefly summarized in this paper, then four examples of ascoma development will be developed before variations of ontogenetical events are considered and concluding remarks exposed.

I - SHORT RECALL OF SOME MORPHOLOGICAL AND STRUCTURAL CHARACTERS OF THE ASCOMA.

Ascomata are usually found on the upper surface of the symbiotic thallus; they can exceptionnally form on the purely fungal hypothallus, for example in some *Rhizocarpon*. Generally, they are either scattered all over the thallus or grouped at its center. Sometimes, they are purely marginal *(Cetraria, Peltigera)*. In *Nephroma*, the mature ascomata seem located at the under surface of the thallus, but, in fact, they form at its margin and turn downwards only later, because the upper side of the ascoma, of thalline aspect, has a more important growth. In some genera *(Cladonia, Stereocaulon, Baeomyces)*, ascomata are born on special formations erected on the thallus (= podetions).

There are two majors morphological types of ascomata: apothecia and perithecia.

Apothecia have a large exposed hymenial surface, usually circular, the **hymenial disc**, surrounded by an **excipular margin** (Fig. 1 A). Their diameter, which is often about 1mm, may be smaller or larger but rarely reaches up 1cm. Apothecia are light-, bright- or dark-coloured, with sometimes differences between the disc and the excipulum. They can be immersed in the thallus (e.g. *Aspicilia)* or superficial. Frequently they have a short stipe, narrower than the disc. Some lichens have apothecia born on podetions. These thallus-like expansions, which are feebly elongated in *Baeomyces*, can reach several centimeters in Cladoniaceae or Stereocaulaceae.

Lirellae, important variant of apothecia, are lengthened ascomata, frequently dark, opening by a longitudinal split; they may be branched (Y- or star-shaped). They are either superficial or immersed in the thallus.

Perithecia are always small, their diameter exceptionnally reaching up 1mm. They appear as black dots on the thallus in which they are generally immersed (Fig. 1 B). At maturity they are flask-shaped with an internal cavity; they usually open by a summital pore (ostiole). Only rarely, they are aggregated in stroma-like structures (Trypetheliaceae, Asterothyriaceae).

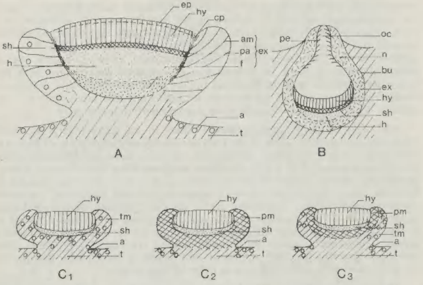

Fig. 1.- Major elements of lichen ascomata. - A- Apothecium: the margin at the right is a typical amphithecium sensu CORNER (1929-1930) without algae, but at the left, it is figured as an amphithecium of thalline appearance including algae. - B- Perithecium. C- C1: lecanorine apothecium ; C2: lecideine apothecium; C3: zeorine apothecium. (Abbreviations: see p. 233).

Ascomata whose characters are intermediate between apothecia and perithecia, are frequently named **"perithecioid apothecia"** (e.g. *Lichina*, some Pertusariaceae and Thelotremataceae).

In ascomata, the **hymenium** is a regular layer of **asci**, which also generally comprises vegetative interascal filaments more or less erected. Those, habitually named **paraphyses**, can however be diverse in their ontogeny. When the summital part of the hymenium is well differentiated, it forms an **epithecium.**

Besides the hymenium, two others main parts have to be distinguished in ascomata; one, beneath the hymenium, contains the sporophytic elements (or their remnants) and can be named the **subhymenium** s. l.*; the other, the **excipulum,** devoided of sporophytic elements, envelops the hymenium and the subhymenium.

The upper part of the subhymenium s. l. is paraphysogenous; it contains the terminal branches of the ascogonial hyphae. Generally well delimited and easily

* The "subhymenium s.l." was originally simply named "subhymenium" by LETROUIT-GALINOU (1967) who was the first to distinguish it from the excipular components by the presence of sporophytic elements.

recognizable, it will be known here as the **subhymenium s. s.***. The lower part of the subhymenium s.l. will be defined as the **hypothecium***; its structure, at its base, often gradually passes to that of the underneath excipulum, so the limit between these two formations is sometimes difficult to distinguish. For some authors (e. g. SIPMAN, 1983), this transitional zone is known as the **subhypothecium**. It must be noticed that in structural descriptions with pure systematic purposes, authors frequently use the term hypothecium to describe the whole underneath part of the ascoma, located under the subhymenium s. s. , making no distinction between its excipular and non-excipular parts.

According to species, the **excipulum** differs by its colour (dark or bright), thickness, aspect (thallus-like or not), texture (fleshy or carbonaceous) and structure (more or less complex). **Lecanorine apothecia** have an excipulum with a thalline appearance (Fig. 1 C_1). **Lecideine apothecia** have an excipulum which is structurally clearly distinct from the thallus (Fig. 1 C_2) and often reminds the hymenial disc; when bright-coloured, **apothecia** are said biatorine. In **zeorine apothecia**, the margin shows two parts, an outer thalline margin of thalline structure and an inner proper margin whose structure differs from that of the thallus (Fig. 1 C_3). Ontogenetically, the excipulum is in fact usually composed of several components, some being early formed (i.e. the floor), other lately developed (parathecium and amphithecium). It will be shown later that parts of the excipulum with similar aspect can differ by their origin.

After developmental studies, several terms, previously used to characterize parts of the excipulum from a purely morphological point of view, have now got a modified sense, for instance, "amphithecium", "periphyses", "subhymenium", "hypothecium" and "podium". So, the term "amphithecium", which was initially applied by lichenologists to any marginal elements of thalline aspect (= thalline margin) and the term "parathecium", which was employed to designate the non-thalline elements of the excipulum (= proper margin), are now used in a restricted ontogenetical sense defined by CORNER (1929 a, b; 1930 a, b, c) (see p. 195 & 213). Consequently, in this paper, the term "amphithecium" will be applied to structural components which may be thallus-like or not (cf. Fig. 1 A). The term "periphyses" has long been used to define short filaments which, in perithecia, may be present in the ostiolar canal and also under the ceiling of the ascomatal cavity; this term must be now restricted to the sole ostiolar filaments (see p. 197 & p. 200).

* For some former authors, the subhymenium s. s. was the "thecogenous layer", the hypothecium was the "subhymenium", the elements underneath their "subhymenium" being the "hypothecium". Some contemporary authors reduce the term "subhymenium" to the subhymenium s.s.

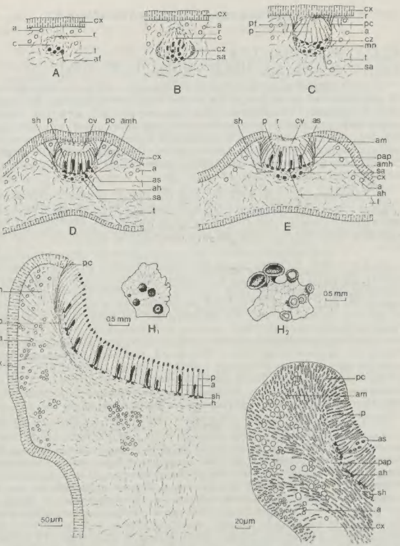

Fig. 2.- *Xanthoria parietina*: ascoma development schematized after JANEX-FAVRE & IBRAHIM-GHALEB (1986) (A to F at the same scale). A- Very young ébauche with ascogonial apparatus; B- Ebauche with circumcentral zone and sporophytic apparatus; C- Older ébauche with parathecioid net and parathecial crown; D- Young ascoma still included in thallus with remnants of the roof over the ascomatal cavity and the developing hymenium; E- Opening of the ascoma and development of the amphithecium; F- Mature apothecium with typical parathecial apparatus; G-Detail of the margin of F; H- Habitus: 1, young stages (A to E); 2, adult apothecium.
(Abbreviations, see p. 233).

II.- EXAMPLES OF ASCOMA DEVELOPMENT.*

A - *XANTHORIA PARIETINA*

(Fig. 2) (after JANEX-FAVRE & IBRAHIM-GHALEB, 1986)

1.- The youngest stage which has been observed, more or less spherical (Ø = 50μm), is located at the base of the thallus algal layer (Fig. 2 A). Its vegetative part is already differentiated into two superposed areas: a plexiform **carpocentrum**, with rather upright filaments, covered by a roof, with more or less horizontal hyphae. **Ascogonial filaments**, with enlarged siderophilic cells, form a knob in the basal part of the carpocentrum. This stage, where the vegetative elements are not all similar but appear differentiated into two parts, will be defined as the **ébauche**** stage.

2.- At a next stage (Fig. 2 B), the older ébauche (Ø = 100 μm) is somewhat piriform because a plexiform growing zone develops at its margin (**circumcentral zone**). Simultaneously, the roof becomes more or less desintegrated by the enlarging carpocentrum. Numerous **sporophytic hyphae** arise from the ascogonial cells.

3.- Later (Fig. 2 C), the top of the ébauche reaches the base of the thallus cortex. Moreover there is a lateral extension of the ascoma, probably due to the activity of the circumcentral zone. Now the carpocentrum has got divided in two superposed parts. The upper one, the **paraphysoid net**, is made of hyphae more or less upright and parallel: the **paraphysoids**. The lower part, meniscus-like, (**basal meniscus**), has a plexiform structure and contains the sporophytic elements in which **ascogenous hyphae**, with croziers, are now distinct. The basal meniscus begins to produce new arising free-ended filaments, the **paraphyses** (= carpocentral paraphyses or primary paraphyses, sensu LETROUIT-GALINOU, 1966). A new formation, the **parathecial crown**, organizes; issued from the top of the circumcentral zone, it is constituted by short free-ended diverging hyphae whose peculiar disposition results from a sympodial mode of growth.

4.- The older ascoma (Ø = 150μm) (Fig. 2 D), remains covered by the thallus cortex. Under some thin remnants of its roof, the paraphysoid filaments have ruptured and an ascomatal cavity develops, being limited at its base by the paraphysis tops. Arising over the laterally extending basal meniscus, the paraphyses are now numerous; they get parallely arranged in a definite layer in which young asci grow up: the **hymenium** is now edificated; so the basal meniscus has to be named **subhymenium** s. l. (the upper part of which, with ascogenous hyphae, being the **subhymenium** s.s.). At the periphery of the ascoma, the subhymenium extends laterally producing hyphae with a subradial disposition. These hyphae are named **amphithecioid hyphae** (see BELLEMÈRE, 1967). In *Xanthoria parietina*, these hyphae, intermingled with algae, get a thallus-like structure and form a verruca around the ascoma. At the margin of

* SANTESSON (1984) is used here as reference for species names.

** "ébauche" is a french word used to define the aspect of a work (as a sculpture for instance) when this is at its beginning, its shape being still unachieved. This term has been prefered to "primary corpus" (LETROUIT-GALINOU, 1968) which may be easily confused, erronously, with "primordium".

the ascoma, the parathecial crown develops basipetally but feebly, its base possibly contributing to the lateral extension of the subhymenium.

5.- The thallus cortex and the remnants of the roof now rupture over the enlarging ascoma; so the ascomatal cavity opens at its top (Fig. 2 E). Lateraly the sympodial growth of the parathecial crown clearly increases: a typical **parathecial apparatus** will now build (Fig. 2 F & G). On its internal face, a few **parathecial paraphyses** develop upwards in a basipetal manner contributing to the lateral extension of the hymenium (and also of the subhymenium). On its external face, the parathecial apparatus generates amphithecial hyphae which compose an **amphithecium** *sensu* CORNER (cf. p. 192). The bases of the parathecial paraphyses and those of the amphithecial hyphae diverge from the **parathecium** *(sensu* CORNER, cf. p. 192); this is a thin sheath made of tangentially oriented hyphae, which lines the subhymenium outside. The amphithecium, in *Xanthoria parietina*, gets a thallus-like structure (with distinct cortex, algal layer and medulla); it contributes to the extension of the verruca which encloses the ascoma and which now projects over the thallus. This verruca has a composite origin; whilst its reduced upper part is made of amphithecial hyphae, its flank is made of amphithecioid hyphae and its basal part of thalline hyphae. Nevertheless, the whole verruca has a thalline-like structure.

6.- Later the parathecial apparatus becomes very important and largely contributes to the widening of the ascoma. At the end, the hymenium is well exposed (Fig. 2 F & G): the ascoma is an **apothecium**. In this, numerous asci have formed on the ascogenous hyphae which extend at the upper part of the subhymenium.

The main characteristics of ascoma development in *Xanthoria parietina* can be summarized as follows:

a) The very young ascoma early differentiates into an ébauche.

b) In the young ébauche, the well-developed carpocentrum is not entirely surrounded by sterile tissues. These are reduced to a transitory roof: the pericentral envelope* is not complete. Around the carpocentrum, a circumcentral zone with a plexiform structure is distinct; it has a growing function.

c) In the older stages, the roof hardly modifies ; the carpocentrum differentiates into two superposed parts: the transitory paraphysoid net, which early makes room to the ascomatal cavity, and the subhymenial meniscus which generates paraphyses (carpocentral paraphyses). Some amphithecioid hyphae form on the external face of the subhymenial meniscus; they take a part in the formation of the verruca which surrounds the young ascoma.

d) A parathecial crown, early distinct above the circumcentral zone, develops in a parathecial apparatus when the ascoma begins to open. This parathecial apparatus plays a major role in the enlargement of the maturing apothecium; its amphithecium has a thalline-like structure.

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* The term "pericentral envelope" is used here preferentially to the anterior term "primary envelope" (LETROUIT-GALINOU, 1968) because it gives a better idea of the location and formation of this envelope and also because it avoids the ambiguity tied to the qualificative "primary".

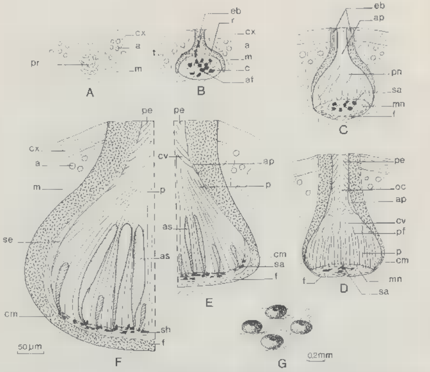

Fig. 3.- *Pyrenula nitida*: ascoma development schematized after JANEX-FAVRE (1971) (A to F at the same scale). A- Young primordium. B- Young ébauche. C- Carpocentrum differentiation . D- Paraphyses and periphyses development. E- Young perithecium. F- Mature perithecium. G- Habitus. (Abbreviations, see p. 233).

B.- *PYRENULA NITIDA* (Fig. 3)
(after JANEX- FAVRE,1971 and HENSSEN & JAHNS, 1974).

1.- Ascoma development begins, in the thallus, at the base of the algal layer, by the formation of a knob of hyphae with a distinct plexiform aspect. This plexus of homogenous structure is a **primordium** still devoided of ascogonial elements (Fig. 3 A).

2.- The young ascoma widens and soon reaches the **ébauche** stage, two parts being now distinct in the ascoma: the **carpocentrum** and the **roof** (Fig. 3 B). In the carpocentrum, the plexiform structure is maintained but a developing ascogonial apparatus is now present. The roof, which covers the carpocentrum, is made of tightened hyphae with thick darkening cell walls. It extends laterally and downwards around the carpocentrum and, at its top, bears a cylindrical bundle of erected filaments, the epicentral bundle which reaches the thallus surfa-

ce. At this stage, the roof is the only element of the pericentral envelope to be present.

3.- The ébauche extends downwards into the thallus. At its base, under the carpocentrum, a clear and thin pale floor made of tangential hyphae develops constituting a second element of the pericentral envelope (Fig. 3 C). Three superposed parts are now distinct in the carpocentrum: its plexiform basal part, or **basal meniscus**, contains numerous sporophytic elements ; its middle part is a **paraphysoid net**; its conical upper part (**apical point**) penetrates upwards into the roof and the overtopping epicentral bundle, and reaches the exterior.

4.- The ascoma, still growing downwards (Fig. 3 D), becomes now flask-shaped; it has a narrow neck and an enlarged bulge with a flat base. Laterally, between the dark roof and the clear floor, a short and thin muff, made of clear tangentially disposed hyphae, differentiates; this **circumcentral muff**, completes the pericentral envelope. In the carpocentrum, the paraphysoid net ruptures near its top: the **ascomatal cavity** appears. The basal meniscus generates upright the first **paraphyses** so the hymenium, still devoided of asci, begins to form. The apical point, inside the darkened epicentral bundle, now shows two regions; the inferior one, at the level of the neck base, remains more or less plexiform; the superior one lyses axially; a narrow ostiolar canal is delimitated, open at its top. This canal is soon lined by short free-tipped filaments turned upwards, the **periphyses**; the lower ones are generated on the remnants of the apical point whilst the superior ones are directly born on the epicentral bundle.

5.- Later, the ascoma becomes higher and broader, its base remaining pale and flat (Fig. 3 E). Its growth, which essentially takes place in the bulge part of the ascoma, seems due to the activity of the clear circumcentral muff. Upgrowing asci born on the ascogenous hyphae infiltrate the numerous paraphyses: the **hymenium** is now typical and the underlaying basal meniscus can be named **subhymenial meniscus**. At the base of the ascomatal neck, the remnants of the inferior part of the apical point vanishes; so, the ostiolar canal, which was open at its top, also communicates now with the ascomatal cavity.

6.- The fully developed ascoma (Fig. 3 F) is a **perithecium** opening by an ostiole at the top of an ostiolar canal. Its neck is relatively short and its enlarged bulge is more or less rounded. The ascomatal cavity is quite entirely filled by the **hymenium**, with numerous paraphyses and mature asci. The subhymenium is reduced to a clear layer containing the ascogenous hyphae. The sterile part of the ascoma, the **excipulum**, now entirely dark, has thickened partly by adjonction of thalline elements; these are especially noticeable at the neck level. Structurally the excipulum wall is complex. Besides its thalline elements, it is made of components of diverse origin: the epicentral bundle is a dependance of the roof, the floor and the hardly distinct circumcentral muff belong to the pericentral envelope; moreover, a thin clear sheath of tangentially disposed hyphae has developed inside the lateral part of the excipulum wall at the hymenium level. This sheath, probably built of peripherical carpocentral remnants, has been named **"secondary envelope"** (JANEX- FAVRE,1971; see p. 209); it possibly produces paraphyses. The periphyses, which are other components of the excipulum, have also different origin; most of them are born on the carpocentral apical point, some on the epicentral bundle and others on the thalline envelope.

Major traits of the ascoma development in *Pyrenula nitida* differs from *Xanthoria* parietina because:

a) a primordial stage is encountered;

b) the ébauche has a more complicated structure. The carpocentrum (well developed) shows an apical point. The primary envelope is complete with a well-developed floor, a reduced muff and an important roof overtopped by an epicentral bundle;

c) the mature ascoma, remaining included in the thallus, is a perithecium with an ostiolar canal lined by numerous periphyses;

d) at the mature stage, ébauche structures are persisting and there are neither amphithecioid nor parathecial elements.

Despite the above differences, there are however some similar characteristics in the ascomatal development of *Pyrenula nitida* and *Xanthoria parietina*. So, in both species:

a) the young ascoma forms into the thallus under the algal layer;

b) there is an ébauche stage with a plexiform carpocentrum and a pericentral envelope;

c) the carpocentrum differenciates into a paraphysoid net and a basal meniscus; this has an important marginal extension;

d) all the paraphyses are generated by the basal meniscus;

e) an ascomatal cavity is formed by the rupture of the paraphysoid net's upper part.

C.- *ENDOCARPON PUSILLUM* (Fig. 4)
(after HENSSEN & JAHNS, 1974 and WAGNER, 1987).

1.- The first stage which has been observed (Fig. 4 A), is a primordium located in the algal layer, underneath the thallus upper cortex. It is a homogenous knob of coalescent filaments whose cells are short and wide. Its basal part contains an ascogonial apparatus made of large siderophilic cells from which trichogynes escape, reaching the upper surface of the thallus. Small algal cells are present in the primordium.

2.- Later on, when the enlarged young ascoma becomes piriform (Fig. 4 B), it is made of three parts and so has reached an advanced ébauche stage. Its summital part, surrounding the degenerating trichogynes, is a conical newly differentiated area made of upright coalescent filaments and originated from neighbouring thalline hyphae; this area is probably an **epicentral bundle** because it is distinctly separated from the carpocentrum by a narrow plate of subtangential hyphae which probably represents a poorly differentiated **roof**. The median part of the ascoma, or **carpocentrum**, derived from the initial knob, is now made of thin filaments; it contains the ascogonial cells. The basal part is interpreted here as the **floor** because its cells differ from the surrounding thallus by their structure and disposition. So, the pericentral envelope is not well characterized, being rather reduced and incomplete (only floor and roof).

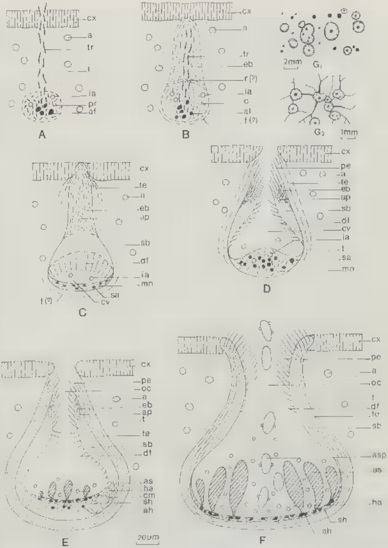

Fig. 4.- *Endocarpon pusillum*: ascoma development schematized after WAGNER (1987) (A to F at the same scale). A- Primordium. B- Young ébauche. C- Older ébauche. D- Opening of the young ascoma. E- Ascoma with young asci F- Mature ascoma. G- Habitus: 1, thalline squamulae on the soil; 2, thallus isolated from the soil. (Abbreviations, see p. 233).

3.- The broadened ébauche (Fig. 4 C), which has elongated both downwards and upwards, now reaches the thallus surface. An **ascomatal cavity** filled with jelly and containing a few small algal cells, has formed into the carpocentrum separating it in two superposed parts which remain in contact only by their margin. The lower part of the carpocentrum, (**basal meniscus**), more or less lenticular, has a plexiform structure and contains fertile elements. The bell-shaped upper part of the carpocentrum (**summital bell**) generates centrifugally free-tipped filaments under its inferior face (**descending filaments**); over its superior face (where the roof is no longer recognizable), an **apical point** of carpocentral origin develops axially in the enlarged epicentral bundle. Around this one, the surrounding thalline hyphae dispose regularly into a peripherical supernumerary envelope (**thalline envelope**) which extends basipetally.

4.- Important modifications of the ascoma structure occur at the next stage (Fig. 4 D). The enlarged ascomatal cavity gets piriform. The basal meniscus which bears no paraphyses, has now a conical shape. Under it, the previously mentioned floor is no longer distinct. Above the cavity, the summital bell and the overtopping apical point have ruptured axially and so an **ostiolar canal** forms which soon opens at its top. On the inferior face of the ruptured summital bell, descending filaments develop, overhanging the ascomatal cavity. Around the ostiolar canal, a thin sheath of rearranged hyphae produces **periphyses**. The lowest ones are born on the upper part of the ruptured summital bell; those, above, are formed on the apical point; near the top of the canal, they form on the epicentral bundle and, at the very top, on the thalline envelope. This one has grown downwards, but does not reach the ascomatal base.

5.- The ascoma, whose growth has been very important (Fig. 4 E), now becomes entirely surrounded by the thalline envelope which darkens at its upper part. Laterally, at the place where the summital bell and the basal meniscus are fusing, a short muff (**circumcentral muff**) has differentiated; it does not bear any filament. The basal meniscus, which has become cupular, does not generate any sterile interascal filaments. The ascogenous cells, present only in the dense upper part of the basal meniscus, produce asci into the ascomatal cavity. Those arrange into a hymenium and so the basal meniscus must now be named **subhymenium** and the summital bell, **subhymenial bell**. Owing to their hyaline aspect and their similar structure, the subhymenial bell, the circumcentral muff and the lower part of the subhymenium constitute a distinct clear peripherical sheath inside the enlarged thalline envelope.

6.- The adult ascoma is a perithecium (Fig. 4 F). In the bulge, the important ascomatal cavity still contains a lot of small hymenial algal cells. At the base of the cavity, the non-exposed hymenium remains devoided of paraphyses. At the top of the cavity, the descending filaments have nearly all disappeared. In the neck, the ostiolar canal is coated by numerous periphyses whose superior ones become dark. The **excipulum** is formed by the dark thalline envelope, now quite complete, and which, inside, has incorporated the sheath of carpocentral origin, observed at the preceding stage.

In *Endocarpon pusillum* and *Pyrenula nitida*, ascomata **are perithecia** with an entirely dark excipulum. In both, the neck, whose components are of various origin, is perforated by an ostiolar canal bearing periphyses. Both, also, are devoided of parathecial elements, oppositingly to the apothecia of *Xanthoria*

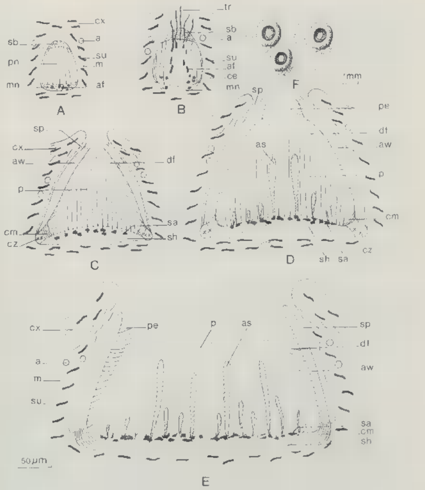

Fig. 5.- *Thelotrema lepadinum*: ascoma development schematized after LETROUIT-GALINOU (1967), HENSSEN & JAHNS (1974), HENSSEN (1976) (A to E at the same scale). A- Young ébauche. B- Ebauche with fully developed ascogonial apparatus and trichogynes. C- Fully developed ébauche with paraphyses, lateral wall and descending filaments. Note its early opening. D- Young apothecium. E- Mature apothecium. F- Habitus. (Abbreviations, see p. 233).

parietina. Nevertheless, *Endocarpon* differs fundamentally from *Pyrenula* by the absence of paraphyses and by the presence of a sushymenial bell producing descending filaments. Moreover, in *Endocarpon*, the primordium is made of

short and wide cells while it is made of intermingled thin filaments in *Pyrenula*. In *Endocarpon*, the dark bottle-shaped excipulum results from the important development of the thalline envelope; in *Pyrenula*, this misses, the excipulum differentiating progressively from the pericentral envelope. During the development of the two species, a clear sheath exists at some stage on the internal face of the excipulum, but it is different by its origin: in *Endocarpon*, it is formed by the carpocentral elements surrounding the cavity and it is transitory, but, in *Pyrenula*, it is a lately formed secondary envelope which persists in the adult ascoma.

D.- *THELOTREMA LEPADINUM* (Fig. 5)
(after LETROUIT-GALINOU,1966; HENSSEN & JAHNS, 1974; HENSSEN, 1976).

1.- The earliest stage which has been observed is a young ébauche (Fig. 5 A), located under the algal layer of the thallus between the suberified cells of the cork. This ébauche shows three superposed zones, all of carpocentral origin, no pericentral envelope being distinct. The lower zone is a **basal meniscus** with a plexiform structure containing a few ascogonial elements; the central zone, more important, is a **paraphysoid net**; the upper zone, formed by coalescent hyphae, is a **summital bell**.

2.- In the increased ébauche (Fig. 5 B), hyphae are now tightened in the lateral part of the young ascoma, so the flank of an envelope of carpocentral origin (**carpocentral envelope**) is differentiating. Ascogonial elements, more or less erected into the paraphysoid net, are now numerous; they bear many trichogynes which, at the top of the ébauche, escape through the summital bell and point out over the thallus.

3.- The older ébauche (Fig. 5 C), remains sunken into the thallus, but opens at its top, rupturing the thallus cortex. Major changes have occurred in the ébauche structure. The carpocentral envelope is no longer distinct, making room to a narrow split which now separates the young ascoma from the thallus. The subhymenial bell has extended downwards; its new-formed part, made of close appressed parallel hyphae tangentially disposed, now constitutes the **ascomatal wall**. On its internal face, this is lined with short filaments, obliquely oriented upwards, their length progressively increasing from the base to the top of the ascoma. Owing to their origin and despite of their orientation, these filaments are **descending filaments**. The paraphysoid net is no longer visible; at its place, upright **paraphyses** have developed, generated by the basal meniscus in which a few sporophytic elements are present. These paraphyses, produced centrifugally, are shorter and shorter towards the margin, forming a conical **hymenium**. In a small area at the base of the ascoma, between the ascomatal wall and the subhymenial meniscus, a peculiar structure appears made, inside, of parallel hyphae disposed similarly to those of a **circumcentral muff** and showing, outside, a plexiform disposition; it constitutes the **circumcentral zone**.

4.- During the ulterior growth (Fig. 5 D), the ascoma continues to push up the surrounding thallus; its form and structure are feebly modified. The hymenium, where young asci develop, widens consecutively to a marginal growth. So does the subhymenium, whose base, however, remains flat. The ascomatal wall extends above the short circumcentral muff which bears no ra-

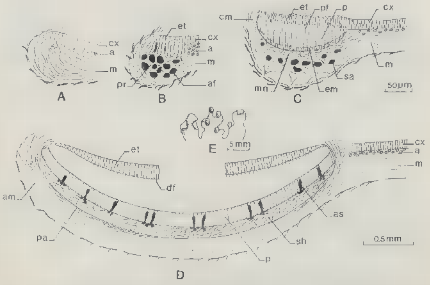

Fig. 6.- *Peltigera rufescens*: ascoma development schematized after LETROUIT-GALINOU & LALLEMANT (1971), HENSSEN & JAHNS (1974), HENSSEN (1976) (A to C at the same scale). A- Sterile thallus margin. B- Primordium. C- Ebauche. D- Opening of the hemi-angiocarpic apothecium. E- Habitus. (Abbreviations, see p. 233).

mification. In its basal part, this grows downwards; at its top, it grows upwards and generates filaments whose length shortens upwards, oppositingly to the underlying descending filaments whose length shortens downwards. As the ascomatal wall is of carpocentral origin, its newly formed top may be considered as an **apical point**; consequently the filaments that it produces, have to be interpreted as **periphyses**. So an **ostiolar apparatus** is present: this is entirely of carpocentral origin (PARGUEY-LEDUC, 1966,1967; JANEX- FAVRE,1971).

5.- The mature ascoma, with a widened and largely exposed hymenium (Fig. 5 E), is an apothecium. The numerous paraphyses have now nearly all the same length, except the marginal ones, so the hymenium has a trapezoidal section. The surrounding thallus, increased in a prominent wart, is separated from the ascomatal wall by the narrow split precedingly mentioned; this has got deeper and more distinct. The apothecium is enlarged by lateral extension of its base, probably due to the generative activity of the persisting circumcentral muff.

The mature ascomata of *Thelotrema lepadinum* and *Xanthoria parietina*, are apothecia, but have a strongly different structure. First, in *Thelotrema lepadinum*, there is no parathecial apparatus. Secondly, the apothecial development exhibits perithecial characteristics, such as the formation of an ostiolar apparatus with periphyses and the development of descending filaments under the sushymenial

bell; however, oppositingly to what happens in typical perithecia, those elements do not overhang the hymenium, but are pushed laterally on its flank. Thirdly, during the apothecial development of *Thelotrema lepadinum*, a paraphysoid net, paraphyses, periphyses and descending filaments are formed; in the three previous examples, none of these structural components were encountered altogether.

Finally, only one character is in common in the development of the four studied examples: the presence of a clearly recognizable ébauche. The importance of the concept of "ébauche" in studies of ascoma development is thus confirmed.

III.- VARIATIONS IN ASCOMA DEVELOPMENT.

The study of the four preceding examples shows that diverse developmental schedules, but also common features exist in lichen ascomatal development. Enlarging the comparisons to other species, considerations will now be developed in attempt to point out the major developmental trends of the sterile components of the ascomata.

Successively will be considered:

A.- Variations during the ascoma edification, i. e. the variations of the **structural elements**, of the **modes of growth**, in the **opening** of the ascomata.
B.- Main characteristics of the mature ascomata.
C.- Main ontogenetical types of ascomata.

A.- VARIATIONS DURING THE ASCOMA EDIFICATION.

1.- Variations of the structural components.

The preceding examples have shown that during the development of the sterile elements of the ascoma, several structurally defined main stages can be observed. These are:

a) the **primordium** stage, in which the sterile elements have an uniform structure;
b) the **ébauche** stage, in which these components begin to differentiate in several parts;
c) the **parathecial stage** in which secondary elements with a sympodial mode of growth develop, forming a **parathecial apparatus**;
d) the **mature stage**, in which no new type of structural element appears (even if the growth goes on).

a) The primordium stage and its structural variations.

The primordium generally forms in the algal layer of the thallus or close to it, either over *(Parmelia)* or under it (*Lecania sulfureofusca*, SIPMAN, 1983). Exceptionnally, it develops on the thallus (*Lichinodium*, HENSSEN, 1981) or in small outgrowths of thallus lobes *(Wavea*, HENSSEN & KANTVILAS, 1985).

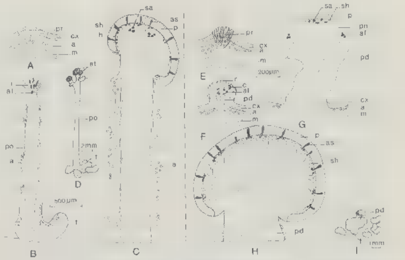

Fig. 7.- A to D. *Cladonia floerkeana*: ascoma development schematized after LETROUIT-GALINOU (1967); see also KRABBE (1891), JAHNS (1970a), JAHNS & BELTMAN (1973) (A to C at the same scale). A- Primordium of podetion. B- Young podetion with young apical ascoma. C-Mature ascoma at the top of a podetion. D- Habitus. E to I. *Baeomyces rufus*: ascoma development schematized after LETROUIT-GALINOU (1967); see also JAHNS (1970a) (E to H at the same scale). E- Primordium. F- Ebauche with carpocentrum. G- Young apothecium with developing hymenium and subhymenium. H- Mature apothecium at the top of a podium. I- Habitus. (Abbreviations, see p. 233).

The primordium can be distinguished from the neighbouring thallus by some histological characters: in most cases, it is a plexus of vegetative hyphae (=generative tissue, HENSSEN and JAHNS, 1974) usually surrounding several ascogonial coils (*Endocarpon pusillum*, Fig. 4 A). It may also differ from the thallus by cytochemical characters (such as gelified walls or cytoplasm reactivity). The primordium generally contains no alga; sometimes, it is the only character which distinguishes the primordium from the thallus as in *Peltigera* (Fig. 6 B), in *Rhizocarpon* and in Lichinaceae.

In some Lichens, mature ascomata are gathered in specialized areas of the thallus. In *Laurera* (JOHNSON, 1940; GALINOU, 1957), *Enterographa* and *Chiodecton*, these areas result from a late coalescence of maturing ascoma elements and are not true stromas preexisting to the primordium formation. Oppositingly to non-lichenized Ascomycetes, primordia of Lichens have never been encountered in, or over, stromas. The defined pulverulent areas on which the groups of primordia of *Phlyctis* are born (LETROUIT-GALINOU, 1967) have not been usually considered as stromatic. The opinion of some authors

(VAINIO,1894; CHADEFAUD, 1984) considering the whole organized lichen thallus as a stroma *per se* can be also mentioned.

Generally the primordium has a plexiform structure; not rarely its hyphae have an arbuscular disposition (*Cladonia*, Fig. 7A). Only exceptionnally, the primordium shows the plectenchymatous structure common to many non-lichenized Ascomycetes *(Arthopyrenia lapponina* and *A. submicans*, JANEX-FAVRE,1971; *Steinera glaucella*, HENSSEN & JAMES, 1982). Sometimes it has been observed, for instance in the genus *Collema* (BAUR, 1898; HENSSEN, 1981), that the vegetative filaments of the primordium are distinctly issued from the foot cells of ascogonial coils.

In the primordium, the sterile filaments generally exist before the ascogonial elements are distinct. It happens however that these are the first to appear (e.g. in Physciaceae and Collemataceae). Eventually, the primordium remains devoided of ascogonial coils, these forming only later, at the ébauche stage, e.g. in *Pyrenula* (Fig. 3 A), *Thelotrema* (Fig. 5 B), some Gyalectaceae (Fig. 9 A) and *Physcia tenella* (OTT, 1987).

In some cases, an ascogonial apparatus develop in a preexisting functional pycnidium: then, no typical primordium is present and the resulting ascoma is known as **pycnocarp** (e.g. *Phylliscіella*, HENSSEN, 1963). New primordia can also appear in ageing ascomata, e.g. in *Lecanora subfuscata* (LETROUIT-GALINOU, 1967), *Baeomyces roseus* (JAHNS & SMITTENBERG, 1970) or some *Caloplaca* (MALONE, 1977).

Generally, the primordium soon differentiates into an ébauche. However, in some cases, the structure of the primordium persists unchanged till the ascoma is mature (e. g. *Arthonia*; cf. HENSSEN & JAHNS, 1974).

The biology of primordia is badly known. Exceptionnaly, authors mentioned that primordia are long-lived (*Megalospora*, SIPMAN, 1983). The physiological conditions of the primordium transformation into an ébauche are unknown; in some cases *(Collema*, BAUR, 1901; *Cladonia*, HONEGGER, 1984) the role of spermatization seems clear.

b) The ébauche stage and its structural variations.

A complex differentiation of the sterile elements of the ascoma takes place at the ébauche stage. It consists, on one hand, in the formation of differentiated **concentric structures:** essentially a **carpocentrum** surrounded by an external **pericentral envelope**. Into each of the concentric constitutive elements, a **dorsi-ventralization** also happens resulting in a storied disposition with distinction of a basal, a median and a tectal parts. So, the **basal meniscus**, the **paraphysoid net**, the **sushymenial bell** individualize in the carpocentrum, while in the primary envelope, the **floor**, the **circumcentral muff** and the **roof**, with eventually its **epicentral bundle**, form. Moreover, a **bilateral symetry** may also appear (primordium of lirellae).

α Variations in the carpocentrum.

At the beginning, the carpocentrum, central part of the ébauche in which are located the ascogonial elements, has the same structure as the primordium. Its differentiation in three superposed parts is usually precocious.

* The **paraphysoid net** proceeds from the median part of the carpocentrum (cf. Fig. 2 A & B, 3 C, 5 A), and is devoided of sporophytic elements. It is generally unique but, in rare cases, several paraphysoid nets may differentiate side by side into the carpocentrum, each of them being later replaced by a distinct hymenium (e.g. in *Pertusaria pertusa*, Fig. 11 K & L). No paraphysoid net forms in the Verrucariaceae where an ascomatal cavity early appears at its place by lysis.

Sometimes, the structure of the paraphysoid net persists unchanged until the ascoma opens (*Opegrapha* (Fig. 10 A-B), *Phlyctis, Gyalectidium)*. Frequently, the paraphysoid net ruptures below the overtopping summital bell, either early *(Lecidella)* or late *(Lobaria)* and a more or less developed ascomatal cavity results. Then, the remnants of the paraphysoid net may vanish or persist in the hymenium as a part of the interascal filaments.

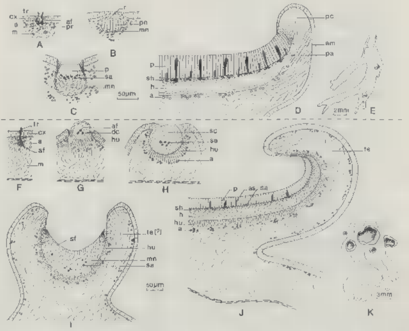

Fig. 8.- A to E. *Ramalina ecklonii*: ascoma development schematized after KEUCK (1979) (A to D at the same scale). A- Primordium. B- Ebauche. C- Very young apothecium. D- Mature apothecium. E- Habitus. - F to K. *Parmelia conspersa*: ascoma development schematized after LETROUIT-GALINOU (1970); see also *P. exasperata* in HENSSEN & JAHNS (1974), HENSSEN (1981) (F to J at the same scale). F- Primordium. G- Developing husk and disappearing carpocentrum. H- Secondary carpocentrum. I- Growing apothecium with upper sterile filaments. J- Mature apothecium. K- Habitus. (Abbreviations, see p. 233).

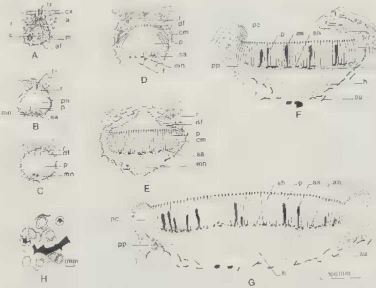

Fig. 9.- *Gyalecta carneolutea*: ascoma development schematized after LETROUIT-GALINOU (1974); see also HENSSEN & JAHNS (1974), HENSSEN (1976) for others Gyalectaceae (A to G at the same scale). A- Young ébauche with trichogynes. B- Carpocentrum differentiation: paraphysoid net and first paraphyses. C- Ascomatal cavity and paraphyses. D- Descending filaments. E- Young apothecium with opening roof. F- Maturing apothecium with, at one side, a developing parathecial crown. G- Mature apothecium. H- Habitus. (Abbreviations, see p. 233).

* The upper part of the carpocentrum, or **summital bell**, is generally thin. In ébauche of **perithecia**, it may produce, upwards, the **apical point** and, downwards, **descending filaments** as in Verrucariaceae (Fig.4 C). When present, the apical point soon dissociates axially and an ostiolar canal results; at its top, this opens out and, at its base, it communicates with the ascomatal cavity. This canal can become lined by **periphyses**. In ébauche of **apothecia**, where the apical point is unknown, descending filaments may exist (Fig. 5 C, 6 D, 9 D); however the presence of a summital bell has not been mentioned under the roof. Descending filaments usually vanish, either early, as in *Lasallia* (JANEX-FAVRE, 1973) or late, as in Gyalectaceae (Fig. 9 G) and Peltigeraceae. They rarely persist; then they generally remain short, e.g. in *Thelotrema* (Fig. 5 E) and *Diploschistes* (HENSSEN & JAHNS, 1974); exceptionnally, however, they may extend downwards through the ascomatal cavity and reach the basal meniscus; then they are known as pseudoparaphyses (*Arthopyrenia lapponina* (= *A. fallax*), *A. submicans*; Fig. 12 A-B).

* The basal part of the carpocentrum or **basal meniscus** which contains the sporophytic hyphae generated by the ascogonial cells, becomes the **subhymenium**

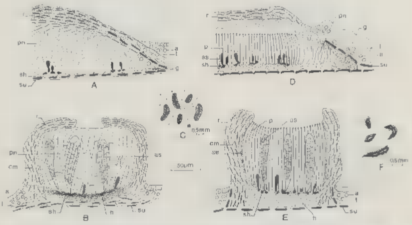

Fig. 10.- A to C. *Opegrapha rufescens*: structure of a lirella schematized after LETROUIT-GALINOU (1967) (A and B at the same scale). A- Extremity of a lirella (longitudinal section). B- Transversal section of a mature part of a lirella. C- Habitus. - D to F. *Graphis scripta* : structure of a lirella schematized after JANEX-FAVRE (1964) (D and E at the same scale). D- Extremity of a lirella (longitudinal section). E- Transversal section of mature part of a lirella. F- Habitus. (Abbreviations, see p. 233).

when the **hymenium** forms. In most cases, the basal meniscus produces upwards free-tipped **paraphyses**; frequently the first paraphyses grow up into the paraphysoid net whose ruptured elements may persist as paraphysoids amongst the layer of paraphyses (*Lobaria*; LETROUIT-GALINOU, 1971). In several families or genera (e. g. Verrucariaceae, Opegraphaceae, Pertusariaceae), the basal meniscus does not generate paraphyses.

* Peripherical hyphae of the carpocentrum sometimes organise in a clear sheath whose structure is distinct from the internal part of the carpocentrum and also from the pericentral envelope. If this structure forms early, it is named the **carpocentral envelope** (e.g. *Verrucaria cazzae*, JANEX-FAVRE,1971; BELLEMERE & LETROUIT, 1988); if it forms lately, it is named the **secondary envelope** (e.g. *Pyrenula nitida*, Fig. 3 F).

β The pericentral envelope and its structural variations.

The pericentral envelope encloses the carpocentrum. Differing structurally from this and from the surrounding thallus, it is always devoided of sporophytic elements; rarely it contains a few algae.

The pericentral envelope is generally present and comprizes three superposed parts: the roof, the median part of the envelope and the floor. It exceptionnaly lacks, the ébauche being only made of the carpocentrum as in *Lecanora subfuscata* (LETROUIT-GALINOU, 1967).

* **The roof.**

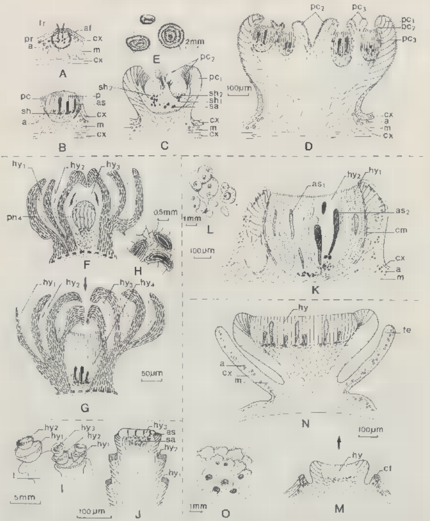

Fig. 11.- A to E. *Umbilicaria cylindrica* schematized after HENSSEN (1970) & JANEX-FAVRE (1974): development of secondary and tertiary lirelliform new apothecia into an initial apothecium (A and D at the same scale). A- Ebauche with a roof. B- Young apothecium. C- Secondary apothecia in a primary one. D- Secondary and tertiary apothecia. E- Habitus. - F to H. *Graphis elegans* schematized after JANEX-FAVRE (1965): successive development of new lirellae in the remnants of an initial one (F and G at the same scale). F- Ebauche of a new lirella into three successive ones. G. Maturation of the new lirella of F. H. Habitus. - I and J. Superposed apothecia successively developed in *Cladia aggregata*: only the last one is fertile (schematized after JAHNS 1970b). I- Habitus. J- Section; note the successive sterile hymenia (hy$_1$, hy$_2$) and the fertile one (hy$_3$). - K to L. Composite apothecium in *Pertusaria pertusa* schematized after LETROUIT-GALINOU (1967). K- New hymenium developed in an old degenerated initial one. L- Habitus. - M to O. Thallus reaction around an apothecium of *Parmeliella coronata* (schematized after HENSSEN, 1969). M- Young apothecium. N- Mature apothecium. O- Habitus. (Abbreviations, see p. 233).

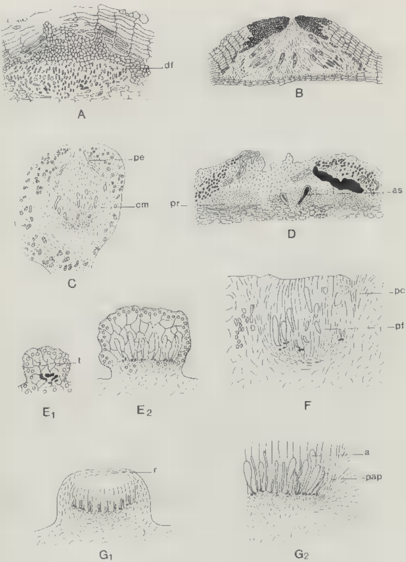

Fig. 12. Some peculiar ontogenetical types in Lichens. A and B. *Arthopyrenia lapponina* (= *A. fallax*) after JANEX- FAVRE, 1971. A- Ebauche stage. B- Adult stage. - C. *Lichina confinis*, schematized after JANEX-FAVRE (1967). - D. *Arthothelium* sp., schematized after HENSSEN & JAHNS, 1974. - E. *Edwardiella mirabilis*, drawn after HENSSEN (1986). - F. *Aspicilia calcarea*, drawn after JANEX-FAVRE, 1985. - G. *Hertella* after HENSSEN 1985. G1- *Hertella chilensis*, young stage. G2- *Hertella subantarctica*, adult stage. (Abbreviations, see p. 233).

- In many Pyrenolichens, the roof, upper part of the pericentral envelope, is generally well developed. Often, as in *Pyrenula nitida* (Fig. 3 B) and in *Endocarpon pusillum* (Fig. 4 B), it grows upwards forming an **epicentral bundle**. This, which incorporates surrounding thalline components, forms the main part of the ébauche neck, around the ostiolar canal (which results from the dissociation of the apical point) and is lined by periphyses.

- In the ébauche of Discolichens (lirellae inclusively), the roof lacks in some genera of various families, e. g. *Arthonia*, *Lecanora*, *Cladonia*. When present, the roof is generally clear and poorly developed. In some cases, it early stops growing and then vanishes as in *Xanthoria* (Fig. 2). The roof is rarely well-developed, being then either light-coloured, as in *Peltigera* (Fig. 6) and *Gyalecta* (Fig. 9) or dark, as in *Graphis* and *Opegrapha* (Fig. 10). The persisting roof ruptures early or late; then, it persists some time before to disappear, as in *Peltigera* (Fig. 6 C); rarely, it is pushed laterally and remains distinct on the flank of the mature ascoma (e. g. *Graphis*, *Opegrapha*, Fig. 10; *Gyalecta*, Fig. 9). No epicentral bundle has been described in Discolichens. However, some formations are perhaps to assimilate to an epicentral bundle, as, for instance, the "epicentral filaments" of *Baeomyces rufus* (Fig. 7 F & G) or also as the parathecial crown which, in some genera, precocely develops at the top of the young ébauche.

* The **floor**, basal part of the envelope, may form somewhat later than the roof, as in *Pyrenula* (Fig. 3 C). It is sometimes lacking, as in *Xanthoria parietina* (Fig. 2 B & C) or in *Thelotrema lepadinum* (Fig. 5 B). In various Graphidaceae, Opegraphaceae (Fig. 10) and Pyrenolichens, the floor is reduced or remains light-coloured whilst the roof is dark and well-developed (dimidiate ébauche). In some cases, the floor develops strongly in a well distinct **podium**; this is clearlight-coloured in *Baeomyces rufus*, (Fig. 7 F to I), but it is black in *Opegrapha calcarea* (CLAUZADE & ROUX, 1985).

* **The median part of the pericentral envelope** is easy to distinguish when it is well-developed and looks like a muff (generally bearing no filaments). This muff is rather long in *Verrucaria cazzae* (JANEX- FAVRE,1971) and in the sides of lirellae (Fig. 10), but it is short in *Pyrenula* (Fig. 3 D). However, when a muff-like structure exists in the lateral part of the ébauche, it has not always a pericentral origin, but may correspond to a carpocentral or a secondary envelope (see p. 209). Ontogenetical studies are therefore necessary to precisely define the structural value of such a convergent type of structures.

In some cases, the median part of the pericentral envelope keeps the juvenile and plexiform structure of the lateral part of the primordium; then it is generally reduced (e. g. *Xanthoria parietina*, Fig. 2 C; *Thelotrema lepadinum*, Fig. 5 C), but it is more developed in the extremities of young lirellae (Fig. 10 A).

Often the median part of the envelope is not distinct.

c) The parathecial stage and its structural variations.

Parathecial formations are not necessarily present. For instance, they do not exist in the Arthoniales, Opegraphales and Graphidales whose mature ascomata remain at the ébauche stage or even at the primordium stage (some Arthoniales). Where they are present, these formations are characterized by a sympodial type of ramification.

* At the beginning, they are always reduced to a **parathecial crown** of divaricated hyphae, located at the margin of the ascoma. The parathecial crown may appear at any ontogenetical stage of development. In some cases (e. g. in *Lecanora* or in *Megalospora*), it forms early around the primordium. Usually it develops at the ébauche stage, either early (e.g. *Xanthoria parietina*, Fig. 2 C), or, more frequently, later, when the roof ruptures, as in *Peltigera* (Fig. 6 D) where the ébauche diameter has reached more than 1mm when the crown forms; then, it appears at the periphery of the subhymenium (e. g. *Gyalecta*, Fig. 9; *Diploicia canescens*, BELLEMERE & LETROUIT-GALINOU, 1988; *Lobaria laetevirens*, LETROUIT-GALINOU, 1971; HENSSEN, 1981).

* Rarely the parathecial formations remain reduced to a parathecial crown (e.g. Gyalectaceae, Fig. 9 G). They generally develop, either early or with some delay (*Xanthoria parietina*, Fig. 2 E to G), into a **parathecial apparatus**. This apparatus is formed by a thin sheath of compact and tangentially oriented hyphae, the **parathecium**, with, inside, an increased production of paraphyses (**parathecial paraphyses**) and, outside, the formation of an **amphithecium** sensu CORNER (1929 a & b; 1930 a, b & c) (cf. p. 192; see also SIPMAN 1983). When the parathecial apparatus is specially developed, a strong lateral amplification of the ascoma results as in many Lecanorales s. l. (e.g. *Xanthoria parietina*, Fig. 2 F; *Ramalina*, Fig. 8 D; *Umbilicaria*, Fig. 11 C; *Parmeliella*, Fig. 11 N). The presence of a parathecial apparatus is generally easy to state because the amphithecial hyphae have a typical sympodial disposition and differ by their aspect from the thalline hyphae (i.e. the lecideine apothecia). But it happens that the amphithecium looks like the surrounding thallus and eventually contains algae, as in lecanorine apothecia (DUGHI 1955) or in immersed ascomata of *Peltigera* (Fig. 6 D) or *Nephroma* (LETROUIT-GALINOU & LALLEMANT, 1970). Meanwhile, in such cases, the parathecial origin of the apothecial margin may be discerned because, at least in its upper part, the sympodial disposition of the hyphae is always clearly distinct (Fig. 2 G).

d) Additional structural components.

Growing reactions may take place in the thallus at some distance around the base of the young ascoma, and may generate additional structures. For instance, in *Thelotrema* (Fig. 5 E) or *Parmeliella* (Fig. 11 N), a cupular formation develops around the ascoma; in *Peltigera polydactyla*, the finger-like part of the thallus bearing the ascoma results from a stimulation of thallus growth located under the apothecium (LETROUIT-GALINOU & LALLEMANT, 1970; JAHNS & FREY, 1982).

2- Modes of growth in the sterile components of ascomata.

a) Growth during the primordium stage.

In the plexiform primordium, growth proceeds by adjonction of elements similar to the preexisting ones; those originates either by intercalary elongation or by ramification of the preexisting primordial filaments, or also by assimilation of

the neighbouring thalline hyphae. When there is an equal and diffuse growth, the shape of the primordium remains unchanged as, for instance, in primordia of perithecia; when the growth is lateraly more important, the primordium becomes discoid. If the renforced marginal growth is limited to some points, the young ascoma turns lirelliform (Fig. 10 C and F, Fig. 11 H) or asteriform. In the primordia of *Cladonia* and *Baeomyces*, horizontal growth is relatively feeble but vertical growth becomes important: a small podetion forms (Fig. 7).

b) Growth during the ébauche stage.

In some cases, the mode of growth of the primordium is maintained during the ébauche stage. More frequently, new areas with peculiar growth differentiate in the ébauche. Generally, these areas only concern a part of the preexisting constitutive structural elements. Each of these areas shows eventually a special modality of growth. Usually, the growth is engaged, either in a perithecial or in an apothecial way, as soon as the ébauche stage.

* **When the ébauche will become a perithecium,** a diametral enlargement affects essentially the bulge part whilst an usually noticeable elongation takes place in the upper part of the ébauche (future neck region); so the young ascoma becomes flask-shaped. In *Pyrenula* (Fig. 3 F) the enlargement of the bulge takes place in the subhymenium and is directed upwards; in *Endocarpon* (Fig. 4 F) it takes place in the margin of the sushymenial bell and is directed downwards. A part of the bulge enlargement may also be due to intercalary growth in the circumcentral muff (old ébauches of *Verrucaria cazzae*, JANEX- FAVRE,1971).

* **When the ébauche will become an apothecium,** the enlargement is essentially located at the periphery of the ébauche (marginal growth), but a diffuse intercalary growth also exists; sometimes, all the structural components of the ébauche have an equal marginal growth; for instance, in *Peltigera* Fig. 6), the paraphysogenous basal meniscus, the paraphysoid net and the roof are similarly affected. In most cases, the extension of each structural component of the ébauche differs; so in *Lobaria*, the widening of the roof early stops, the paraphysoid net feebly grows on laterally while the floor and the meniscus strongly extend becoming concave (Fig. 13 A); in *Diploicia canescens*, (cf. BELLEMERE & LETROUIT, 1988), the roof and the paraphysoid net do not enlarge (and quickly vanish); only the basal meniscus and the floor extend, their newly formed parts being known as the "proparathecium" (LETROUIT-GALINOU, 1967).

* **The lengthening of the ébauche of a lirella** (Fig. 10) is due to the persistance at its extremities of the type of growth established in the primordial stage. Oppositingly, on the flank of the lirella, the restricted diametral growth is probably consecutive to the differentiation of the muff (Fig. 10).

* Ebauches of **perithecioid apothecia,** show simultaneously apothecial and perithecial types of growth, the modalities differing with species. For instance, in *Thelotrema* (Fig. 5), the enlargement of the ébauche at its base is as important as in an apothecium, but at its upper part there is a strong vertical elongation as in a young perithecium. In *Lichina* (HENSSEN, 1963; JANEX-FAVRE, 1967), the roof does not develop (as it generally does in a young apothecium) but the lateral extension of the meniscus and of the floor is reduced (as in a perithecium).

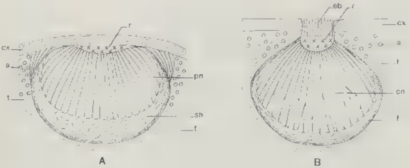

Fig. 13.- Comparison of ascoma and conidioma ébauches in *Lobaria laetevirens* schematized after LETROUIT-GALINOU (1971, 1972). A- Ascoma ébauche. B- Conidioma ébauche. (Abbreviations, see p. 233).

* Sometimes, certain parts of the ébauche have a peculiar growth. For instance, in *Baeomyces* (Fig. 7), the meniscus and the floor thicken strongly and a podium results. In *Verrucaria cazzae*, a special and important growth of the upper part of the neck occurs and an involucrum develops (cf. BELLEMERE & LETROUIT, 1988).

c) Growth during the parathecial stage.

When the sympodial mode of growth characterizing the secondary formations of ascomata is important, with formation of a complete parathecial apparatus, there is a marginal growth which can lead to a strong diametral enlargement of the ascoma (e. g. *Xanthoria, Parmelia, Usnea*). Oppositingly, when only a parathecial crown develops, the marginal sympodial growth is reduced; then it is the type of growth established in the ébauche which is the major cause of the enlargement of the maturating ascoma *(Gyalecta,* Fig. 9; *Pachyphiale cornea,* LETROUIT-GALINOU, 1977).

d) Special localized growths.

New vegetative growth points, with a restricted importance, sometimes appear externally on thallus-like amphithecium; they may produce different types of marginal hyphae (as ciliae in *Usnea* or as excipular irregularities in *Lecanora allophana)*.

3 - Variations in the modalities of opening in ascomata.

According to species, the opening of the ascoma takes place at different stages of the development.

* When no roof develops in the young ascoma (e.g. *Cladonia* (Fig. 7 A), *Lecanora, Arthonia)*, or if the roof vanishes early, before the beginning of the hymenium formation (e.g. *Nephroma, Lecidella, Ramalina*, Fig. 8 B-C), the development of the ascoma is said **gymnocarpic**. One must keep in mind that gymnocarpy is independant of an eventual persistance of thalline elements over the developing ascoma.

* If the roof ruptures after the hymenium is constituted, but before it contains mature asci, the ascoma is said **hemiangiocarpic**, e.g. *Peltigera* (Fig. 6), *Gyalecta* (Fig. 9), *Stereocaulon* (WOLFF, 1905; JAHNS, 1970a), *Diploicia* (LETROUIT-GALINOU, 1967).

* The ascoma development is said **angiocarpic** if the roof lately persists, till many mature asci are present in the hymenium. This is the case of perithecia (e.g. *Pyrenula*, Fig. 3 and *Endocarpon*, Fig. 4); these generally open by an ostiole formed at the top of the neck; when, rarely, perithecia open by a simple hole, then there is no neck (*Arthopyrenia halodytes*, JANEX-FAVRE, 1971). Lirellae (e.g. *Opegrapha, Graphis*, Fig. 10) are also angiocarpic: they open by a longitudinal split which is apparently devoided of some special dehiscence mechanism, oppositingly to some non lichenized Discomycetes *(Lophodermium)*. Angiocarpic apothecia are apparently very rare in Lichens; they are however encountered in several non-lichenized Discomycetes *(Phacidium)*.

In some cases, it may be difficult to clearly assign the development to a gymno-, a hemiangio- or an angiocarpic type. For instance in *Phlyctis* and *Roccella* (LETROUIT-GALINOU, 1967), as in *Dirina* (TEHLER, 1983) and in *Lecanactis* (HENSSEN & JAHNS, 1974), there is a persisting roof over the hymenium as in angiocarpic types, but its peculiar structure allows spore release through it.

4. Repeated development of ascomata.

In some lichens, new apothecia may form on, or in developing ones according to different processes. For instance, in *Graphis elegans* (Fig. 11 F & G), the repeated lirellae develop from new ébauches which successively differentiate inside the preceding ones, probably in areas where the sporophytic apparatus is locally reactivated. In Umbilicariaceae (Fig.11 A to D), the new secondarily developed apothecia also form around reactivited parts of the sporophytic apparatus, but, in this case, the initial apothecium has developed from a complete ébauche whilst the secondary apothecia (which become lirelliform) are, from the beginning, only constituted of parathecial structures. In *Pertusaria pertusa*, new ascomata, reduced to a more or less extended hymenium, here and there differentiate into old degenerated hymenia (Fig.11 K). Clearly, such ascomata are ontogenetically distinct from those which, in the same genus, result from the formation of several paraphysoid nets in one single ébauche (see p. 208). In *Cladia*, with storied apothecia these are devoided of asci except the last one (Fig. 11 I & J).

B. VARIATIONS IN THE ADULT STAGE.

1. The realization of the adult ascomata.

The ascoma is adult when its sterile components have got their definitive structure: no new structural elements being added later; however the ascomatal growth can still go on for some time.

The developmental stage at which the ascoma reaches its mature structure differs according to species. For instance, the mature ascoma keeps the structure of a primordium in *Arthonia* (Fig. 12D); it has the structure of an ébauche in *Thelotrema* (Fig. 5), *Opegrapha* (Fig. 10), *Graphis* (Fig. 10), *Pyrenula* (Fig. 3); it has that of a stage with a marginal parathecial crown in the Gyalectaceae (Fig. 9) or in some *Lichina* (HENSSEN & BÜDEL, 1984); it reaches a stage with a developed parathecial apparatus in *Xanthoria* (Fig. 11) and many Lecanorales s. l. (LETROUIT-GALINOU, 1967; HENSSEN & JAHNS, 1974).

Frequently structural components can have disappeared at the adult stage whatever the stage they individualize in the ascoma development. Examples are: the roof in *Xanthoria parietina*, (Fig. 2 A to E); *Peltigera*, (Fig. 6); *Gyalecta*, (Fig. 9 A to F) or the descending filaments of the lateral part of the envelope in *Endocarpon* (Fig. 4 C to E) or in some Gyalectaceae (Fig. 9 D to F).

2. Structural differences in the adult.

a) The excipulum.

Since a long time, morphological excipular characters (consistance, colour, aspect of hyphal walls), which largely differ according to species, have been used in systematics. Later, structural characters have been considered at a great extend. However, one must keep in mind that, structurally, the excipulum may be composed of several elements which have differentiated at diverse stages of the development. Those are: the pericentral envelope (and also the carpocentral envelope or the late secondary envelope), the amphithecioid hyphae (generally appeared at the ébauche stage), the amphithecium and the parathecium (which form at the parathecial stage). Moreover, thalline elements may also add to the excipulum at any stage in the development. This diversity and complexity of the structural composition of the excipulum, can be illustrated with four examples. For instance, in *Endocarpon* (Fig. 4), the excipulum essentially comprizes the thalline envelope and the remnants of the epicentral bundle. In the Graphidaceae and the Opegraphaceae (Fig. 10), the excipulum is made of the persisting pericentral envelope, laterally thickened with black amphithecioid hyphae. In *Diploicia canescens* (cf. BELLEMERE & LETROUIT-GALINOU, 1988), the excipulum is composed by remnants of the pericentral envelope, amphithecioid hyphae and a complete parathecial apparatus with a black amphithecium. In *Xanthoria parietina* (Fig. 2 F), the purely parathecial excipulum, is made of a thin parathecium and of a thick amphithecium of thalline aspect. Owing to this

complexity, the excipulum structure has to be used in systematics only after precise ontogenetical studies.

Thin external hyphae are sometimes produced downwards by the excipulum. They may plunge into the underneath thallus and eventually reach the substratum. These hyphae which can be associated in bundles, contribute to anchor the ascoma and perhaps also to feed it (e.g. Collemataceae, HENSSEN, 1981; Megalosporaceae, SIPMAN,1983). As already mentioned, the excipulum may also produce ciliae or have an irregular outline.

b) The subhymenium s.l. .

The subhymenium s. l. may remain thin, as in *Pyrenula* (Fig. 3) and *Thelotrema* (Fig. 5), but is generally relatively thick. Its upper part (the **subhymenium** s.s.) contains the ascogenous hyphae and is thin. Its lower part, the **hypothecium**, more or less developed, is specially thick in most Lecanorales s.l. where it progressively incorporates the paraphysis bases (LETROUIT-GALINOU, 1967). The limit between the hypothecium and the floor of the primary envelope is often difficult to discern, specially when both are darkened. So one must be cautious in using hypothecial anatomy as a systematical character.

c) The hymenium.

Interascal filaments are generally numerous; rarely there are only a few (*Phylliscíella*, HENSSEN & BÜDEL, 1984); sometimes, they completely lack as in *Endocarpon* (Fig.4 F) and the Verrucariaceae.

* There are several types of interascal filaments according to their **origin:**

- **paraphyses** (i.e. erected hyphae) are produced, either by the basal meniscus of the ébauche (primary paraphyses: LETROUIT-GALINOU, 1961) or by the inner part of the parathecium (secondary paraphyses*: LETROUIT-GALINOU, 1961);

- **paraphysoids** result of the rupture, near their top, of the constitutive elements of the paraphysoid net (*Opegrapha*, Fig. 10 A & B; *Roccella*, LETROUIT-GALINOU, 1967; *Dirina*, TEHLER, 1983; *Lecanactis*, HENSSEN & JAHNS, 1974);

- **residual persisting hyphae of the primordium,** only slightly streched by the growth of the asci, become interascal filaments in some rare cases, e. g. *Arthonia* (HENSSEN & JAHNS, 1974);

- **vegetative thallus hyphae,** merely modified in their wall aspect and pigmentation rarely become interascal filaments and only in thallinocarpic ascomata (e. g. *Rhizocarpon*, HONEGGER, 1978);

- **pseudoparaphyses** (i.e. elongated descending filaments) exceptionally form in Lichens (JANEX- FAVRE,1971);

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* This term has been also used later to qualify the free-tipped filaments lately formed in pycnocarps (HENSSEN, 1963)

- **conidiophores,** functional or not, may become the initial interascal filaments of ascomata resulting from pycnidial transformation (pycnocarps). Such conidiophores have been sometimes ambiguously named "primary paraphyses" (HENSSEN, 1963);

Several types of interascal filaments may coexist in one single ascoma (some Graphidaceae).

* **The aspect** of the interascal filaments, which strongly differs in Lichens, results from their differentiation in the course of their development and is largely independant of their origin. Frequently, interascal filaments are very thin and slender. Sometimes, they are stiff, with a thick wall of cartilaginous appearance (e. g. *Aspicilia*, ROUX, 1977). They may be simple or branched or variously anastomosed. In *Lichina* (HENSSEN et al., 1985), they are moliniform at their top. Conidiogenous paraphyses have been exceptionnally mentioned (*Thelotrema lepadinum*, LETROUIT-GALINOU, 1967). In Lichens, interascal filaments are generally embedded in an abundant hymenial jelly which is often iodine reactive and makes the hymenium compact (e.g. *Psora*, TIMDAL, 1984b); it may eventually contain oil droplets (e.g. some Trypetheliaceae and Megalosporaceae). The upper part of the layer of interascal filaments is frequently differentiated in an epithecium. This generally results from the embedment of the modified tips of the filaments by rather dark pigments. Sometimes, the epithecial layer only consists of a deposit of substances (e.g. calcium oxalate, lichen phenols) over the top of the interascal filaments. In *Phlyctis*, the epithecium is of a different origin; it results from the persistance above the interascal filaments of cells pertaining to the ascomatal roof. The reactivity of the epithecium to certain chemical agents is frequently used as a test for diagnosis. Free tips of the interascal filaments overtopping the epithecium, or presence of cristal deposits over the hymenium, may give a pruinose aspect to the hymenial surface.

* **Modalities of growth** are poorly known in interascal filaments. Their elongation contributes to increase the thickness of the subhymenium rather than that of the hymenium whose height generally remains unchanged during the maturation of the ascoma. In the Caliciales, paraphyses can have unlimited growth (TIBELL, 1984).

Generally, asci begin to appear early, before the ascoma is adult (*Xanthoria*, Fig. 2 D). In some cases, however, the fully-developed ascoma remains long devoided of mature asci, for instance in *Lecidella elaeochroma* (GALLOE 1927; LETROUIT-GALINOU, 1967), *Lecidea fusco-atra* (HERTEL, 1977) and in *Hypocenomyce* (TIMDAL, 1984a). Usually, asci are present in the whole hymenium; eventually they may be absent in its axial part where persisting tightened sterile filaments, similar to paraphysoids, form a pillar-like structure (*Thyrea rotunda*, HENSSEN & BÜDEL, 1985).

* **Algae** are present in the hymenium of a few genera (*Endocarpon*, Fig. 4 F; *Staurothele*). These hymenial algae are smaller than thallus algae; they however belong to the same species, but exhibit characters of the non-symbiotic state (WAGNER, 1984).

3.- Structural characters of the main types of mature ascomata.

a) Perithecia.

The **excipulum** of perithecia is generally entirely dark. It may lack or remain pale at the base (dimidiate perithecia); it is entirely pale in *Dermatocarpon*. The structural components of the perithecial excipulum differs according to species: e.g. primary and secondary envelopes in *Pyrenula nitida* (Fig. 3), thalline envelope in *Endocarpon* (Fig. 4). The neck surrounding the ostiolar canal of the perithecia is more or less developed; it eventually extends in an involucrum which may be important (*Staurothele sapaudica*, JANEX-FAVRE, 1976; *Verrucaria cazzae*, cf. BELLEMERE & LETROUIT, 1988). **Periphyses** line the ostiolar canal: the upper ones are directly born on the epicentral bundle, the lowest ones are produced on the ruptured part of the summital bell and on the remnants of the apical point. In perithecia, **interascal filaments** are generally paraphyses (*Pyrenula*, Fig. 3); pseudoparaphyses are very rare (*Arthopyrenia submicans*, JANEX- FAVRE,1971); paraphysoids are exceptionnaly present (e.g. Trypetheliaceae, GALINOU, 1957). In pycnocarps, the interascal filaments may be eventually persisting conidiophores. Interascal filaments are lacking in Verrucariaceae. **Asci** are generally relatively numerous in perithecia; in nearly all cases, they are of the bitunicate-fissitunicate type even if the interascal filaments are paraphyses.

b) Lirellae.

The **excipulum** of the lirellae, generally black and well-developed, is made of intermingled coalescent hyphae with thick and dark wall. The basal excipulum may develop in a more or less important podium (e.g. *Opegrapha calcarea*, CLAUZADE & ROUX, 1985); it is missing in dimidiate lirellae (e. g. *Opegrapha saxatilis)*. Excipulum is quite reduced or entirely lacks in Arthoniaceae. **Interascal filaments**, always present in lirellae of lichens, can be either paraphyses *(Graphis)* or paraphysoids *(Opegrapha)*; interascal pseudoparaphyses and descending filaments are unknown. An epithecium is exceptionnaly developed which may be pruinose or eventually bright coloured *(Arthonia cinnabarina)*. Enchased lirellae are known in some species (e.g. *Graphis elegans*, Fig.11 F to H).

c) Apothecia.

Excipulum of apothecia, generally fleshy, has rarely a carbonaceous texture. In Gyalectaceae (Fig. 9 G), the excipulum is formed by the parathecial crown and possibly by some remnants of the roof; in most Lecanorales, it is generally a part of the parathecial apparatus. Thalline aspect of the excipulum may be due either to a thalloid structure of the amphithecium (*Xanthoria*, Fig. 2) or to an additional thalline envelope (*Parmeliella diplomarginata*, Fig. 11 N). **Interascal filaments** are always present in apothecia; they are generally paraphyses; more rarely they are thalline hyphae, as in thallinocarps, or paraphysoids as in *Aspicilia*. When there is a distinct **stipe**, this is either a local swelling of the thallus (some *Lecanora*) or the thickened floor of the primary envelope (podium: e.g. *Baeomyces*) or also a part of the hypothecium (some *Lecidella)*.

Although they are thallus-like, the podetions are ontogenetically a part of the ascoma (except perhaps in Stereocaulaceae); in Cladoniaceae, they result of an important vertical elongation of the whole primordium (Fig. 7 B); in Baeomycetaceae, the podetions are thickened podia (Fig. 7 G).

d) Perithecioid apothecia.

Perithecioid apothecia are of two different types. One is encountered in Thelotremataceae where the disc, large as in apothecia and made of paraphyses, is surrounded by the sushymenial bell (the so-called ascomatal wall) and by a persistent surplumbing apical point as in perithecia (Fig. 5). The other type of perithecioid apothecia exists, for instance, in *Lichina pygmaea* (HENSSEN, 1963; JANEX-FAVRE, 1967; HENSSEN et al., 1985) or in *Pertusaria pertusa* (Fig.11 K). There, the hymenium, which contains paraphysoids, is narrow, as it is in perithecia, and is more or less enclosed in a well-developed circumcentral muff (generating externally thalloid amphithecioid hyphae); however the disc is exposed as in an apothecium.

C - ONTOGENETICAL TYPES OF ASCOMATA

From the combination of the precedingly described possible structural variations and types of growth during ascomatal development, a great number of ontogenetical types result. Some of these deserve special interest, either because they are frequent or because they show some remarkable features. They will be considered now.

1.- Types without any differentiation of a parathecial apparatus.

Most of these types have a perithecial type of mature ascoma, but some have a perithecioid apothecium or an apothecium.

a) Types with perithecia.

α) The *Verrucaria* type (cf. BELLEMERE & LETROUIT, 1988).

This type, illustrated in the present paper by *Endocarpon pusillum* (Fig. 4), was first recognized by DOPPELBAUER (1959) and then confirmed by JANEX-FAVRE (1971) and HENSSEN & JAHNS (1974). Its main characters are: a plexiform primordium, the absence or quasi-absence of paraphysoids in the ébauche, the existence of short descending filaments, the absence of paraphyses (or, if present, lately and poorly developed). The adult perithecium has a well developed ostiolar apparatus. The stage which precedes the formation of asci is characteristic (verrucariacean stage) (WAGNER, 1987). Variations are limited; they concern the constitution of the ascomatal wall, the importance of the involucrum and also the eventual presence of paraphyses which has been mentioned by some authors (*Verrucaria (Amphoridium) calcicedum*, DOPPELBAUER, 1959; *Verrucaria controversa*, JANEX-FAVRE, 1970; *Thelidium immersum*, DOPPELBAUER, 1959; *Thrombium aoristum*,

CLAUZADE & ROUX, 1985). The *Verrucaria* type is encountered in a large range of lichen genera, presently included in the Verrucariaceae; it was unknown in non-lichenized Pyrenomycetes till it has been recently recognized in Herpotrichiellaceae (JANEX-FAVRE, 1988). Owing to the presence of a large and early formed ascomatal cavity with short descending filaments and without paraphyses, the *Verrucaria*-type has been often included in the Ascoloculares (SANTESSON, 1950; JANEX-FAVRE, 1970). This however has been questioned because the ascomatal cavity does not form by lysis and also because the primordium has a plexiform structure, a character considered as ascohymenial by HENSSEN & JAHNS (1974).

In *Arthopyrenia lapponina* (= *A. fallax*) and *A. submicans* (JANEX-FAVRE,1971), the ascomatal ontogeny is a variant of the *Verrucaria*-type, but rather distant owing to the non-plexiform structure of the primordium and to the well-developed descending filaments becoming later interascal filaments. The ébauche stage reminds that of the Microthyriaceae (Pleosporales) (Fig. 12 A-B).

β) The *Pyrenula* type (Fig. 3).

In this type, paraphysoids are well-developed in the ébauche and numerous paraphyses are present at the adult stage. An internal and late developed secondary envelope forms which lately is included in the excipulum. An ostiolar apparatus may be present or not. Some *Porina*, i.e. *P. heterospora* (= *P.nucula* HENSSEN & JAHNS, 1974; HENSSEN, 1976), *P. byssophila* (JANEX-FAVRE, 1981), some *Acrocordia*, i.e. *A. conoidea* (JANEX-FAVRE,1971) and some *Arthopyrenia*, i.e. *A. sublittoralis* (JANEX-FAVRE,1971) are probably to be included in this type. A few minor variations are known in the *Pyrenula* type (cf. JANEX-FAVRE, 1971).

γ) The *Trypethelium* type.

This type, also observed in *Laurera*, is probably to distinguish from the *Pyrenula* type, because the interascal filaments are paraphysoids (JOHNSON, 1940; GALINOU, 1957); however new precise developmental datas are needed.

b) Types with perithecioid apothecia.

α) The *Pertusaria* type (Fig. 11 K).

The primordium is plexiform. Paraphysoids are present in the ébauche, and persist as interascal filaments after the roof has disappeared. The ascomatal wall, lately formed, consists in a secondary circumcentral muff (cf. p. 212);the mature ascoma, included in a thalloid verruca, is more or less perithecioid (KRABBE, 1882; LETROUIT-GALINOU, 1967; HENSSEN & JAHNS, 1974).

β) The *Lichina* type (Fig. 12 C).

In this type, similar to the *Pertusaria* type, some periphysoid filaments form a reduced ostiolar apparatus, reminding that of typical perithecial types. All the Lichinaceae are not of this type (HENSSEN, 1963; HENSSEN et al., 1985).

γ) The *Thelotrema* type (Fig. 5).

Numerous paraphyses are present. The ascomatal wall, built from the sus-hymenial bell of the ébauche (Fig. 5) bears descending filaments and an ostiolar

apparatus with periphyses is present at its top. This type, characteristic of the Thelotremataceae (g. *Thelotrema, Diploschistes, Ocellularia)*, reminds one of the ascomatal development in the major genera of the Stictidaceae, a mostly non-lichenized family.

c) Types with apothecia (or lirellae).

α) The thallinocarp type.

In thallinocarps, there is no differentiated primordium, the asci form in certain parts of the thallus where hyphae get slightly differentiated, becoming the interascal filaments. This type seems to exist in some Lichinaceae as *Edwardiella* (Fig. 12 E) (HENSSEN, 1986) and *Lichinodium* (HENSSEN, 1963, 1981), but is in doubt in *Lichina* (see above). *Rhizocarpon* has been mentioned to belong to this type (HONEGGER, 1978), but the mature ascomata, with an apparent margin, have probably a more complicated structure than thallinocarps.

β) The *Arthonia* type (Fig. 12 D).

In this type *(Arthonia, Arthothelium ...)*, the hyphae of the plexiform primordium get rearranged in the hymenium when asci develop, and become paraphysoid-like threads. There is no differentiated ascomatal wall. The mature ascoma may be circular, lirelliform or asteriform. First described as typically ascolocular (SANTESSON, 1950), this type is more recently considered as ascohymenial (HENSSEN & JAHNS, 1974).

γ) The *Opegrapha* type (Fig. 10 A to B).

The plexiform primordium extends in an horizontally elongated ébauche. This differentiates into a meniscus and a paraphysoid net and becomes surrounded by a distinct envelope. The mature ascoma is a lirella with no ostiolar apparatus, opening by a split; its interascal filaments are paraphysoids. This type of development is somewhat alike that of *Therrya fuckelii*, a non-lichenized Ascomycete (BELLEMERE, 1967). In *Roccella montagnei*, the development, difficult to interprete, is perhaps a variant of this type.

δ) The *Graphis* type (Fig. 10 D to F).

The young stages remind those of *Opegrapha*, but later typical paraphyses develop; in the mature lirelliform apothecia there are no descending filaments nor ostiolar apparatus. Some *Tholurna* (Caliciales) (HENSSEN & JAHNS, 1974; TIBELL, 1984), are perhaps a variant of this type with a developed stipe. Types reminding that of *Graphis* are known in some non-lichenized Ascomycetes, but with some differences: in *Rhytisma acerinum*, there are short descending filaments whilst in *Pseudopeziza* and *Bulgaria*, the mature apothecia is not lirelloid (BELLEMERE, 1967); moreover the latter has an important gelatinous stroma.

ε) The *Baeomyces* type (Fig. 7 E-I).

The important primordium has a plexiform structure; its lower part elongates upwards in a podium; at its upper part, under a thin veil (= roof), a net of hyphae containing ascogonial coils differentiates. Later, upright filaments develop at the top of the net through the veil; only those surrounding the asci, become paraphyses.

2. Types with differentiation of a parathecial apparatus.

a) Types with a parathecial apparatus reduced to a parathecial crown.

α) The *Aspicilia* type (Fig. 12 F).

It is characterized by the precocious differentiation of a marginal parathecial crown around the primordium. This crown remains reduced in the subsequent development. The interascal filaments are reputed to be paraphysoids.

β) The *Gyalecta* type (Fig. 9).

Paraphysoids, which exist in the young ébauche, disappear in the old ones. Numerous paraphyses develop. Some short descending filaments are also present. After the subcircular opening of the ébauche, the persisting roof is pushed lateraly on the flank of the developing ascoma; then it generally disappears, replaced by a parathecial crown which takes no part in the subsequent ascoma enlargement. A similar type of development is known in non-lichenized Ascomycetes (e. g. *Calloria*, BELLEMERE, 1967)

b) Types with a typical parathecial apparatus.

α) The *Peltigera* type (Fig. 6).

At first, the primordium has a thalline structure; later it becomes a typical ébauche with a paraphysoid net. This ébauche enlarges whilst numerous paraphyses and descending filaments develop. At last, the roof vanishes; a well-developed parathecial apparatus differentiates at the margin of the hymenium and takes a large part in the peripherical extension of the apothecium.

β) The *Diploicia* type (LETROUIT-GALINOU, 1961, 1967; HENSSEN 1968; cf. BELLEMERE & LETROUIT, 1988).

The primordium has a plexiform structure. The young ébauche, with a paraphysoid net, enlarges only by its basal part which forms a lateral pro-parathecium. Then the paraphysoid net ruptures near its top and an ascomatal cavity develops under the roof; paraphyses and asci are generated by the subhymenium. Later the roof vanishes; a peripherical parathecial apparatus differentiates, widening the apothecium. A similar hemi-angiocarpic development, frequent in Lichens, exists, for instance, in *Hertella* (HENSSEN, 1985 b), *Polychidium* (KEUCK, 1977), *Lobaria* (LETROUIT-GALINOU, 1971; KEUCK, 1977; HENSSEN, 1981) and in *Lasallia* (HENSSEN, 1970; JANEX-FAVRE, 1973). It is also known in *Umbilicaria* (HENSSEN, 1970; JANEX-FAVRE, 1974), where, moreover, secondary hymenia form (Fig. 11 A to D; cf. p. 216) and in Stereocaulaceae, where apothecia develop on thallus expansions miming the typical podetions of Cladoniaceae (WOLFF, 1905; JAHNS, 1970 a).

γ) The *Xanthoria* type (Fig. 2).

In this type, the ébauche is characterized by the early formation of a parathecial apparatus with a tendancy to a precocious gymnocarpic ascoma. The parathecial apparatus plays an important role in the growth of the ascoma. A number of slight variants are encountered, for instance in *Buellia (excl.*

Diploicia), *Lecanora*, *Lecidea*, *Lecidella*, *Parmeliella*, *Lecania*, *Megalospora*, *Ramalina* (LETROUIT-GALINOU, 1967; HENSSEN, 1968; KEUCK, 1977, 1979; SIPMAN, 1983). They differ by the reduction of the ébauche, the importance and details in the structure of the parathecial apparatus.

The *Diploicia*- and the *Xanthoria*-types (= parathecial types, BELLEMERE, 1967) are well-represented in the non-lichenized Ascomycetes.

c) **Peculiar types with presumably atypical parathecial apparatus.**

In these types, difficulties of interpretation arise because dispositions of hyphae encountered in certain structural components, at definite stages of the development, are not alike those which are usually observed at such stages in the same components, but they more or less remind one of dispositions generally encountered either at other stages or in other structural components.

α) The *Cladonia* type (Fig. 7 A to D).

The initium of the podetion which will bear the hymenium, is arbuscular. It can be interpretated either as a non typical primordium or as a precocious parathecial crown developed on a primordium very reduced (more than in *Xanthoria parietina*). With the first hypothesis, the resulting podetion has to be interpreted as an elongated carpocentrum (LETROUIT-GALINOU, 1967); with the second hypothesis (CHADEFAUD et al., 1969), it would be equivalent to the parathecial discopodium described in various stipitate apothecia of non-lichenized Discomycetes (cf. BELLEMERE, 1967).

β) The *Parmelia* type (LETROUIT-GALINOU, 1970; HENSSEN & JAHNS, 1974).

Known in the genera *Parmelia* (Fig. 8, F to K), *Usnea*, *Evernia*, *Cetraria*, this type shows a plexiform primordium which quickly vanishes whilst a paraplectenchymatous husk forms at its periphery. Later, paraphyses are produced on a plexus generated on the internal face of the husk. The origin of the husk is a subject of controversy. According to HENSSEN & JAHNS (1974) and HENSSEN (1981), the husk derives from the external part of the primordium; consequently it should have to be considered as a part of a pericentral envelope. According to LETROUIT-GALINOU (1970), the inwards growth of the husk results from a parathecial structure located at the margin of the primordium; so this husk would be a new formation, added to the primordium, and would represent the internal part of a strongly modified parathecial apparatus. This parathecial hypothesis seems to be more appropriate as *Parmelia* asci are similar to those of *Lecanora*, a genus in which the ascomatal development is accelerated, with no recognizable ébauche and with the formation of a precocious parathecial apparatus. The *Parmelia* type of development could represent an accelerated (more evoluted ?) *Lecanora* type.

From these two examples, *Cladonia* and *Parmelia*, the question of possible convergences in ascomatal development arises. At the present time, this question cannot be correctly answered as detailed ontogenetical studies are still insufficient; consequently this problem will not be further developed here.

It has been mentioned above that some of the ontogenetical types of lichen ascomata remind of those known in non-lichenized Ascomycetes. However, the

types encountered in some major taxa of lichens, are frequently original and unknown in non-lichenized Ascomycetes. Such are, for instance, the *Pyrenula* type and its variants in the Pyrenulales, the *Peltigera* type of the Peltigeraceae, the *Parmelia* type of the Parmeliaceae sensu HENSSEN & JAHNS (1974). Oppositingly, ontogenetical types common in non-lichenized Ascomycetes are rare or unknown in lichens, as for instance, the *Dothidea* type (with nutritious cells), the *Nectria* type, the discopodial type of the Helotiales. Nevertheless, same fundamental processes in ascomatal development exist in the Ascomycetes, lichenized or not. The originality observed in Lichens, may result either from the persistence of primitive traits (i.e. Graphidaceae comparitively to Rhytismataceae) or from a specific evolution towards types whose setting up is favoured by lichenized life (e. g. Cladoniaceae, Parmeliaceae, Peltigeraceae).

IV.- FINAL CONSIDERATIONS.

Stimulating hypotheses concerning the evolution of Ascolichens can be elaborated from structural and ontogenetical datas relative to ascomata (see HENSSEN & JAHNS, 1974; SIPMAN, 1983; HERTEL, 1984). These hypotheses however have to be compared with those resulting from the consideration of others components of the developmental cycle: vegetative apparatus, conidiomata and fertile elements, specially asci.

The processes of hyphal differentiation occuring in ascomatal ontogeny have to be interpreted by comparison with the development of the non-lichenized mycelium and with the thallus edification. On these problems, new concepts and interesting hypotheses have been recently developed (see CHADEFAUD, 1960, 1984; HENSSEN, 1963; LETROUIT-GALINOU, 1969; LALLEMANT, 1983, 1985; WAGNER & LETROUIT, 1988).

Similarities between the development of ascomata and conidiomata have been recognized in non-lichenized Ascomycetes (CHADEFAUD 1965, 1982 a). In Lichens, they have been mentioned by LETROUIT-GALINOU (1972, 1984) who observes, that during the development of *Lobaria laetevirens* (Fig. 13), a system of diverging hyphae extends between a reduced roof and a developed floor as well in the young ascoma as in the young conidioma; in the ascoma, these hyphae become paraphysoids; in the pycnidium, they become branched conidiophores. However, the growth is mostly marginal in the ascoma whilst it is basilar in the conidioma.

The correlations between the development of the sterile elements of the ascoma and that of the sporophytic apparatus have not been clearly established. However, in some cases, a regulation seems to exist: so, in *Parmelia conspersa*, ascogonial elements are only observed in the primordium, whilst the sporophytic elements are only found in the basal meniscus, the dicaryotic cells forming later, when the paraphyses establish. Generally, the development of the asco-sporophytic apparatus is too poorly known to allow any valuable conclusion.

Ascomatal characteristics have for long been largely used in Lichen systematics. At first, only morphology and general anatomy have been taken into account; then detailed structure and histology of the hymenium and

subhymenium were specially considered. Nowadays, ontogeny is recognized to have the best systematical value amongst ascomatal criteria and so this has led, either to reconsider families, or to split some of them or also to join some to others. For instance, the Opegraphaceae have been separated from the Graphidaceae, the Baeomycetaceae and the Stereocaulaceae have been excluded from the Cladoniaceae; oppositingly, the Usneaceae have been joined to the Parmeliaceae (cf. HENSSEN & JAHNS, 1974), and genera precedingly placed in different orders are now gathered in Lichinales (HENSSEN & BÜDEL, 1988).

Important elements to our knowledge of evolutive traits in the Lichens have been also brought by the study of the fine structure and development of asci (BELLEMERE & LETROUIT, 1987). Recently, several lichen families have been redefined and numerous new ones built by the consideration of ascal structure (HAFELLNER, 1984). It appears that evolutive trends in Lichens would be more accurately defined if systematical divisions are founded altogether on ascal and ascomatal datas. Consequently, it would be desirable that in the same family, genera have similar ascal type and similar ascomatal ontogeny. This is effectively satisfied in the new delimitation of the Parmeliaceae which joins, for instance, *Parmelia, Usnea* and other genera. Another example is the justified reestablishment of the Ramalinaceae differing from the Parmeliaceae by ascomatal ontogeny (Fig. 3) and also by the ascal apex structure. But rather frequently ascal and ascomatal datas lead to antagonistic systematic conclusions. Then, other characters must be considered to delimit taxa. For instance *Endocarpon* and *Dermatocarpon*, which have similar bitunicate asci and were precedingly placed in the same family (Verrucariaceae); however they differ in their ascomatal development (WAGNER, 1987); differences in their conodioma types (JANEX-FAVRE and WAGNER, 1986), argues to place them in two distinct families, respectively the Verrucariaceae and the Dermatocarpaceae (WAGNER, 1987).

Outlines of ascomatal evolution in Lichens will not be discussed here, the purpose of the present paper being restricted to expose some reflective considerations concerning the development of the ascomata. We only hope to have shown that datas relative to ascomatal ontogeny, though they are long and difficult to obtain, are fundamental for a better knowledge of evolutionary trends in Lichens and higher Ascomycetes.

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LIST OF ABBREVIATIONS USED IN THE FIGURES 1 to 13.

a, algae; af, ascogonial filaments; ah, ascogenous hyphae; am, amphithecium; amh, amphithecioid hyphae; ap, apical point; as, asci; asp, ascospore; at, ascomata; aw, ascomatal wall; bu, bulge; c, carpocentrum; ce, carpocentral envelope; cm, circumcentral muff; cn, diverging conidiophores; ct, thalline envelope initium; cv, ascomatal cavity; cx, thallus cortex; cz, circumcentral zone; dc, disappearing carpocentrum; df, descending filaments; eb, epicentral bundle; ec, epicentral cone; em, ectal meniscus; ep, epithecium; et, ectal part of the primordium; ex, excipulum; f, floor; g, growing zone; h, hypothecium; ha, hymenial algae; hu, husk; hy, hymenium; i, initium of the ascomata; inv, involucrum; lm, lateral muff; m, thallus medulla; mn, meniscus; n, neck; oc, ostiolar canal; p, paraphyses; pa, parathecium; pap, parathecial apparatus; pc, parathecial crown; pd, podium; pe, periphyses; pf, paraphysoid filaments; pm, proper margin; pn, paraphysoid net; po, podetion; pp, proparathecium; pr, primordium; r, roof; rh, rhizomorph; sa, sporophytic apparatus; sb, sushymenial bell; sc, secondary carpocentrum; se, secondary envelope; sf, sterile filaments; sh, subhymenium; sp, split; su, suber; t, thallus; tm, thalline margin; te, thalline envelope; tr, trichogyne; sf, sterile filaments.

ADDITIONS AND CORRECTIONS FOR PHILIPPINE MOSS FLORA

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ABSTRACT - *Bryobrothera crenulata* (Broth. et Par.) Thér., *Bryum erythropilum* Fleisch., *B. clavatum* (Schimp.) C. Muell., *Diaphanodon blandus* (Harv. in Hook.) Ren. et Card. var. *recurvedentatus* Zant., *Entosthodon physcomitrioides* (Mont.) Mitt., and *Philonotis socia* Mitt. are reported new to the Philippine moss flora. In addition, four new synonyms are proposed for the genus *Bryum* Hedw., and one new combination, *Anomobryum erectum* (Broth.) Tan et T. Kop. is made.

Owing to its geographic location and geologic history, the Philippine archipelago has received its moss taxa from several sources: East Asiatic mainland, maritime Pacific coast, the Himalayas, tropical Asia, Australasia and Oceania, not to mention the widespread northern and southern temperate taxa (Tan 1984).

The study of Philippine moss flora started near the turn of this century when several European and North American explorers and naturalists collected in the Philippines. The results which were published in widely scattered journals were ably summarized by Bartram (1939). In spite of this, later collections continue to yield new records including several species new to science. The recent checklist by Iwatsuki and Tan (1979) includes 625 species belonging to 218 genera.

Progress of Philippine bryology has been specially rapid in the last ten years. This is evident in the discoveries of twelve genera new to the country: *Physcomitrium, Hageniella, Orthodontium* (Iwatsuki & Tan 1980), *Orthorrhynchium* (Tan 1981), *Dixonia, Meteoriella, Mnium* (del Rosario & Van Zanten 1982), *Tristichella* (Tan & Iwatsuki 1983), *Haplohymenium, Solmsiella, Leptostomum* (Tan 1987) and *Grimmia* (Tan & Deguchi 1987).

No doubt, future exploration in remote mountains on distant islands in the country will expand substantially the size of this diverse flora. Such exploration is most necessary because of the on-going destruction of the local forest vegetation.

Below we present 5 species as noteworthy additions to the Philippine moss flora. *Bryobrothera* Thér. is a new generic record. In addition, four new synonyms are clarified and proposed for the genus *Bryum* Hedw. One new combination is likewise made in *Anomobryum* Schimp. Specimens of these new records are deposited at the herbaria of the University of the Philippines at Los Baños (CAHP) and the University of Helsinki (H).

Bryobrothera crenulata **(Broth. et Par.) Thér.**
Rev. Bryol. 47: 26. 1920.

The discovery of this species in the mountains of Mindanao Island is a remarkable extension of another Australasian floral element into the southern Philippines. For that matter, the species is a new record for the western Malesian subprovince.

Bryobrothera crenulata has an interesting history having been described at various times as a member of *Mesochaete*, *Calomnium* and *Rhizogonium* (Norris & Robinson 1979, Koponen et al. 1986). Its biosystematic position and familial status has only recently been clarified (Norris & Robinson 1979). As a member of Hookeriaceae, it was missed out in the recent revision of the family for the Philippine moss flora (Tan & Robinson 1989).

Locally, this species forms extensive mats covering the branches of tree in *Agathis-Podocarpus* montane forest and appears superficially like a hepatic.

Dr. D. Norris kindly confirmed our determination of the Philippine specimen of *Bryobrothera crenulata*.

Specimen examined: Mindanao Is. Mt Hilong-Hilong, Cabadbaran, Agusan Norte Province, Tan & Navarez 84-520 (CAHP, H). New Philippine generic and species record!

Genus *Bryum* Hedw.

This large and difficult genus is poorly understood and equally undercollected in the Philippines. Iwatsuki and Tan (1979) listed 11 species with two endemic taxa: *B. microtheca* C. Muell. and *B. chrysobasilare* Broth. 1908, non Broth. 1924. Unfortunately, these two Philippine endemics were overlooked by Ochi (1985) in his summary revision of subfamily Bryoideae for South, Southeast and East Asia. Nor were the two taxa mentioned by the same author in his earlier studies (Ochi 1959, 1960, 1968a, 1970).

We examined the types and reference collections of *Bryum microtheca*, *B. leucophyllum* Dozy et Molk. and *B. chrysobasilare* and interpreted the first two taxa as synonyms of *B. argenteum* Hedw., and the last one synonymous to *B. erythrophyllum* Fleisch.

We also studied the type of *Bryum erectum* Broth. and found it conspecific with *B. petelotii* Thér. et Henry. Earlier, Bartram (1939) had synonymized *B. erectum* with *B. microtheca*, a conclusion with which we disagree.

Likewise, we studied the Philippine specimens of *Bryum australe* Hampe cited in Bartram (1939) and would consider them *B. paradoxum* Schwaegr. sensu Ochi (1985).

Lastly, *Bryum clavatum* (Schimp.) C. Muell. sensu Ochi (1985) was identified from a recent collection made by the first author from Mindoro Island (Figs. 1-5).

The detailed information is as follows:

Bryum argenteum **Hedw.**
Sp. musc. frond.: 181. 1801.

Bryum microtheca C. Muell., Syn. musc. frond. 1: 314. 1848. **syn. nov.** - Type: Philippines, Manila, Meyer s.n. (not seen).

Bryum leucophyllum Dozy et Molk., *Ann. Sci. Nat. Bot.* sér. 3, 2: 301. 1844. **syn. nov.** - Type: Java, no collector (isotype, H-BR!).

There is a wealth of discussions on the gametophytic variation of *Bryum argenteum* (Fleischer 1902-1904, Sainsbury 1955, Nyholm 1958, Gangulee 1974, Scott & Stone 1976, Crum & Anderson 1981, Frahm & Frey 1983), but curiously, little attention is given to the sporophytes which have been assumed to be uniform in this species.

We attempted to fill this gap of sporophytic information by studying two large population of *Bryum argenteum* collected from a burnt and cultivated limey outcrop in Trinidad Valley, Benguet Province, Luzon Is. (Tan 86-465, 86-461, CAHP, H). The two populations were selected on the basis of their relatively uniform gametophytes which clearly identify them as the var. *lanatum* (P. Beauv.) Hampe.

In both populations, the number of suberect or slightly inclined capsules in the semi-dry state were calculated to be about 10% based on a total of randomly selected 50 capsules in each population. The rest are either horizontal or pendant with various degrees of angle formed between the theca and the seta.

Subsequently, five suberect to weakly inclined capsules were chosen and dissected for peristomial details. The results were then compared with the peristomial structures observed in five pendant capsules. True enough, there is a trend in the reduction of peristomial structures from the perfect type seen in typical, pendant capsules to the variously imperfectly developed types seen in the suberect capsules.

It appears that the tiny transverse bars or appendiculae of the endostomial cilia are the first to disappear in a non-pendant capsule. This is followed by a reduction of cilial length. In both suberect and pendant capsules, the endostomial segments are rather fragile, often left broken in the long dehisced capsules.

The opercular lid, likewise, was observed to vary from markedly apiculate to nearly flat with only a vestigial hump. Length of thecae varies between 1-2mm and the setal length measures from 10-20mm. The variable characters mentioned in this paragraph, however, have no correlation with the posture of the capsules. On the other hand, exothecial cells and stomatal apparati are observed to be rather uniform in all capsules studied.

Thus, the separation of *Bryum leucophyllum* from *B. argenteum* on the basis of characters such as appendicular versus nodulose cilia, and apiculate versus blunt opercular lid (Fleischer 1902-1904, Ochi 1985) is clearly untenable.

Similarly, *Bryum microtheca*, which was separated from *B. argenteum* by characters such as suberect or pendant capsules and reduced cilia (Mueller 1848, Bartram 1939), is equally an ill-founded species.

We think that it is best to combine these three taxa. Although we failed to locate the C. Mueller's type of *Bryum microtheca*, the reference specimens so named at the Brotherus Herbarium, including an isotype of *B. leucophyllum*, support our view.

Bryum erythropilum **Fleisch.**
Musci Buitenzorg 2: 553. 1904. - Type: Indonesia, West Java, Tjibodas, Fleischer s.n. (syntype, H-BR!).

Bryum chrysobasilare Broth., *Philipp. J. Sci.* 3 *C*: 19. 1908, **syn. nov.** - Type: Philippines, Luzon Is., Mt. Data, Merrill 4956 (holotype, H-BR!).

Bryum erythropilum was reduced to a synonym of *Bryum clavatum* (Schimp.) C. Muell. by Koponen and Norris (1984) who had adopted a broad species concept for the genus because of the great variation seen in their large New Guinean moss collections. Ochi (1985), however, maintains the two as separate species on the bases of their differences in sexuality (autoicous in *B. erythropilum* and dioicous in *B. clavatum*), in the degree of leaf border differentiation (1-2 rows of elongate border cells in *B. erythropilum* versus 2-5 rows of linear border cells in *B. clavatum*), and also in the size of median to basal leaf cells (longer and larger in *B. clavatum*). Seen in this light, the type of Philippine *B. chrysobasilare* is conspecific with *B. erythropilum*.

On the other hand, the remarks made by Bartram (1939) regarding the colored basal leaf cells and deep red capsules of *B. chrysobasilare*, in our evaluation, has little taxonomic value. The same features are seen in *B. clavatum* sensu stricto and also in *Bryum paradoxum* (see below).

In addition, numerous deep red, sphaerical rhizoidal gemmae of different sizes were observed in the other Philippine specimen of *B. erythropilum* (Tan et al. 84-380).

Specimen examined: Mindanao Island, burnt mossy forest near the peak of Mt Kitanglad, Butuan Province, mixed with *Funaria hygrometrica*, Tan, Navarez & Amoroso 84-380 (CAHP, H). New Philippine species record!

Bryum paradoxum **Schwaegr.**
Sp. musc. frond. Suppl. 3: 224a. 1827.

Bryum "tenuisculum" Hook. in Iwatsuki et Tan, *Kalikasan* 8: 186. 1979, error pro *Bryum teretiusculum* Hook., Icon. Pl. 1: 20f. 1836, synonymized by Ochi (1969).

Bryum australe Hampe sensu Bartram, *Philipp. J. Sci.* 68: 141. 1939.

Bartram (1939) cited two Philippine collections of *Bryum australe* (Williams 1782, 3148, H-BR) and corrected the species determination to *B. ambiguum* Duby (= *B. apiculatum* Schwaegr.). Our examination of these two collections shows that the specimens have strongly excurrent leaf costae. The leaf cell areolation consists of narrowly rhomboidal to elongate-linear upper and median leaf cells that are (60-)75-135(-150)μm long, with sharp angular ends and thin-walled, and becoming abruptly broadly rectangular at base. The leaf margins are weakly serrulate towards the apex, consisting of 1-3 rows of linear border cells, and are partly revolute. These characters suggest to us that these two Philippine collections are *B. paradoxum*.

Bryum paradoxum differs from *B. apiculatum* principally in having a much stronger excurrent leaf costa, less concave leaves and more revolute leaf margins.

On the other hand, it differs from the true *Bryum australe*, according to Ochi (1970, 1985), in having longer excurrent leaf costae and a more or less abrupt transition of leaf cell shape from the elongate cells in the upper 2 3 of the lamina to broadly rectangular ones near leaf base. Ochi (1985) considers the two as vicarious taxa in temperate Asia and Australasia.

Bryum paradoxum can also be confused with *Bryum erythropilum*. Based on our limited experience with the Philippine specimens, the former is best distinguished from the latter by its longer leaf cells in the upper half of the lamina, and by a revolute and more strongly differentiated leaf border consisting of 1-3 rows of linear cells, instead of the 1-2 rows of rectangular to elongate leaf border cells seen in *B. erythropilum*. Ochi (1985) further distinguishes the two taxa by their sexuality, autoicous in *B. erythropilum* and dioicous in *B. paradoxum*.

Bryum paradoxum is a variable species. Defined in a broad sense, it can be considered a synonym of *B. clavatum* sensu Koponen and Norris (1984). We have, however, not seen enough material of *B. paradoxum* to offer a definitive taxonomic judgement on this matter. Ochi (1985) distinguishes *B. paradoxum* from *B. clavatum* mainly because of the presence of a more markedly differentiated leaf border in *B. clavatum*.

The biosystematic relationship among these four taxa needs more clarification. Ochi (1970, 1985) has illustrated well his concepts for these four species.

Specimens examined: 1) *Bryum paradoxum* - Luzon Is., Benguet Prov., Baguio, on rock, Williams 1782 (H-BR); ibid, Sablan, on rock, Williams 3148 (H-BR). 2) *Bryum clavatum* - Mindoros Is., Mt Halcon vicinity, Tan 87-042 (CAHP, H). New Philippine species record!

Anobryum erectum **(Broth.) Tan et Kop.,** ***comb. nov.***

Basionym: Bryum erectum Broth., *Philipp. J. Sci.* 3 C: 19. 1908. - Type: Philippines, Luzon Is., Benguet Province, Kabayan, Merrill 4968 (holotype, H-BR!).

Bryum petelotii Thér. et Henry in Henry, *Rev. Bryol.* n. sér. 1: 43. 1928, **syn. nov.** - Type: Vietnam, Tonkin, massif du Pia-Quac, dv. Cao-Ouac, Petelot s.n. (isotype, H-BR!).

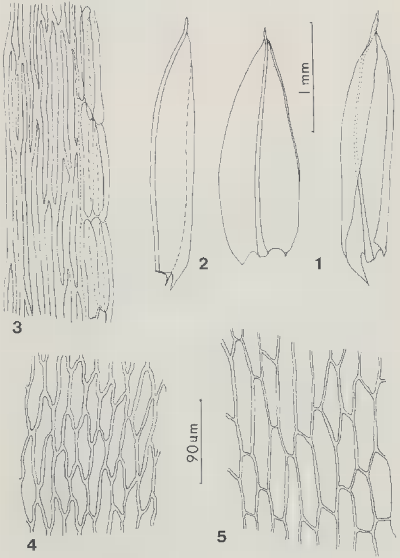

Fig. 1-5. *Bryum clavatum* (Mindoro, Mt. Halcon, Tan 87-042): 1 & 2. Leaves; 3. Leaf border; 4. Upper leaf cells; 5. Lower leaf cells.

The types of these two bryaceous taxa described with erect capsules match perfectly in both their gametophytic and sporophytic details. Chronologically, *Bryum erectum* has priority over *B. petelotii*.

Although the type specimen of *Bryum erectum* has silvery, terete branches with leaves that closely resemble that of *Bryum argenteum*, the two species can be separated by several characters. In *B. erectum*, the median and submedial leaf cells are oblong-rhomboidal to spindle-linear shaped, measuring 60-130μm long, with sharp terminal ends and thin-walled. In *Bryum argenteum*, they are shortly oblong to rectangular, mostly 30-50μm long, with blunt cell ends and moderately thick-walled. Additionally, the leaf costa of *B. erectum* is percurrent to only weakly excurrent from a gradually acuminate leaf apex. Contrastingly, in *B. argenteum*, especially the var. *lanatum*, the leaf costa is strongly excurrent, filling the subula of the abruptly contracted cuspidate leaf apex. Indeed, even under a 10x field lens, the piliferous hairpoints are more clearly visible in *Bryum argenteum* than in *B. erectum*. Most importantly, the capsules of *B. erectum* are erect and somewhat oblong, reminiscent of the capsular type of *Brachymenium* or *Anomobryum*.

In discussing the placement of *Bryum albo-imbricatum* Ochi (syn. *B. albidum* Broth. in Herz., 1916, hom. illeg.) from Bolivia, Ochi (1980) disagreed with Brotherus (l.c., see protologue) who allied this taxon to *Bryum argenteum* on the basis of their gametophytic similarity. Instead, because of exothecial cell characters, Ochi (1980) considered it to be a member of his subgenus *Anomobryum*. According to him, these cells in *Bryum albo-imbricatum* are more or less elongate-rectangular with uniformly thick walls except near the oral region of the capsule. In *Bryum argenteum* and its allies, the exothecial cells are mostly narrowly rectangular with very thick vertical walls, becoming abruptly hexagonal to short rectangular with thin cell walls near the oral region.

Interestingly, the same differences exist in the exothecial cell morphology between *Bryum erectum* and *B. argenteum*. Further comparison of capsules of some species of *Anomobryum* and *Bryum* made by us shows that in *Bryum*, there are 1-4 rows of horizontally oriented, narrowly rectangular shaped cells bordering the capsular mouth. In *Anomobryum*, the oral border of the capsule appears to consist of only 1-2 rows of such type of exothecial cells.

Bryum erectum is, extraordinarily, the only species among the Southeast and East Asiatic members of Ochi's subgenus *Bryum* (1985) that has erect capsules. Also, its upper leaf cells tend to be more linear-elongate than usual in *Bryum*. Furthermore, the leaf costa of *B. erectum* is without guide cells. We are, for all these reasons mentioned above, accepting *Bryum erectum* as an *Anomobryum* sensu Koponen and Norris (1984).

Admittedly, species of *Anomobryum* with long acuminate leaf apices are rare, but not unknown. In addition to *Anomobryum albo-imbricatum* (Ochi) T. Kop. et Norris cited above, we can mention *Anomobryum kasmirense* (Broth.) Broth. from the Himalayas.

Bartram (1939) seem to have overlooked these critical morphological differences when he synonymized *Bryum erectum* with *B. microtheca* (= *B. argenteum* in this paper). Of the four collections Bartram (1939) listed under *B. microtheca*, only the two specimens from Kabayan town (Merrill 4968, Bacani, For. Bur.

15988, H-BR) are truly *Anomobryum erectum*. The other two are typical of *Bryum argenteum* var. *lanatum*.

On several occasions, Ochi (1954, 1959, 1963a, 1985) has suggested that *Bryum petelotii* (= *Anomobryum erectum*) resulted from an intergeneric cross between *Bryum argenteum* and *Brachythecium exile* (Dozy et Molk.) Lac. He supported his claim by evidence of aborted spores, among others. However, spores from the Philippine specimens of *Anomobryum erectum* which measure 6-9μm in diameter appear highly viable. Furthermore, a few Philippine plants were observed to bear axillary globose bulbils measuring 180-250μm long and 120μm wide.

The range of *Anomobryum erectum* now includes several localities in warm temperate Asia and tropical Asia, reaching as far as Costa Rica and Mexico (see Ochi 1985).

***Diaphanodon blandus* (Harv. in Hook.) Ren. et Card. var. *recurvedentus* Zant.**
Blumea 9: 544. 1959. - Type: India, Sikkim, Kurseong, Decoly & Schaul 2564 (isotype, H-BR!).

This variety was described to consist mainly of long, flaccid and flagelliform stems and branches with few lateral innovations. The leaf margins are coarsely serrated with patent to recurved teeth (Van Zanten 1959). Although flagelliform modified branches are seen also in specimens of var. *blandus*, they are never so profusely developed as in the present variety.

Despite the remarkable morphological distinction, we think that the var. *recurvedentatus* is probably a widespread eco-variety caused by the shade and highly humid condition at high elevation.

Diaphanodon blandus var. *recurvedentatus* has been recorded only from Sikkim (Van Zanten 1959). We have now seen many more specimens of this variety, including an isotype, at the Brotherus Herbarium. The total range of it can be gleaned from the specimens cited below and this includes a new Philippine record.

Specimens examined: India, Manipur, 1899, Fraser s.n. (H-BR); Upper Burma, near Ruby mine, Olivier s.n. (H-BR); Sri Lanka, Kirigalpota, Herzog 80a (H-BR); Indonesia, Java, Pangerango, 1897, Möller 139 (H-BR); Philippines, Luzon Is., Benguet Prov., Mt Santo Tomas, 30 Nov. 1986, Tan s.n. (CAHP, H).

***Entosthodon physcomitrioides* (Mont.) Mitt.**
J. Linn. Soc. Bot. Suppl. 1: 55. 1859.

The key and illustrations to the species of *Entosthodon* (Ochi 1986b) works well with the Philippine specimen. However, the leaf apices of Philipppine *E. physcomitrioides* vary from piliferous to short acuminate, with more leaves on the piliferous side. Length of capsules also varies from 1.5 to 2mm. Like all other members of the genus, the local populations of *E. physcomitrioides* grow on disturbed clayey road cut along a mountain cliff.

Entosthodon dozyanus C. Muell. from Java differs from the present species in having a markedly differentiated leaf border and a capsule with only short neck.

Presently, *Entosthodon physcomitrioides* has a known distribution from India, Indochina, Taiwan and New Caledonia (Ochi 1968b). Its presence in the Philippines is not totally unexpected.

Specimen examined: Luzon is., Benguet Prov., Buguias, on way to Ballay, Tan & Hernaez 85-123 (CAHP, H). New Philippine species record!

Philonotis socia **Mitt.**
J. Linn. Soc. Bot. 8: 151. 1864.

The key and illustrations prepared for the species of *Philonotis* Brid. in Ochi (1962, 1963b) and Iwatsuki and Mizutani (1972) should be consulted for the differences between *P. socia* and its related taxa.

Among the Philippine congeners, *Philonotis socia* is characterized by a lanceolate-triangular leaf outline with predominantly short rectangular basal leaf cells and a short excurrent leaf costa. The leaf margins are strongly revolute nearly throughout.

The local habitat is a wet, partly shaded rocky ledge at the mouth of a spring in a newly opened forest clearing.

The range of *Philonotis socia* now covers Japan, Taiwan, China mainland, India and the Philippines.

Prof. Z. Iwatsuki of Hiroshima University kindly confirmed our species determination.

Specimen examined: Luzon Is., Laguna Prov., Louisiana, Tan 84-37 (CAHP, H). New Philippine species record!

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LIQUENES CON CIANOFICEAS DE CAAVEIRO, LA CORUÑA (N-O DE ESPAÑA)

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RESUMEN - Continuamos dando a conocer los resultados del estudio sobre la flora liquénica de la "fraga" de Caaveiro (La Coruña), reuniendo en este trabajo los taxones pertenecientes a las familias: Collemataceae Nannf., Lichinaceae Chev., Lobariaceae Chev., Pannariaceae Tuck. y Peltigeraceae W. Watson. Consideramos especies interesantes: *Polychidium dendriscum* (Nyl.) Hensen, nueva cita para Europa continental; *Pannaria tavaresii* P.M. Jørg., nueva cita para España peninsular; *Leptogium microphylloides* Nyl. y *Parmeliella jamesii* Ahlner & P.M. Jørg. muy poco citadas en España. Otras 8 especies son novedades para la flora de Galicia.

ABSTRACT - New results of the study on the lichen flora of the "fraga" of Caaveiro (La Coruña).The taxa of the families: Collemataceae Nannf., Lichinaceae Chev., Lobariaceae Chev., Pannariaceae Tuck. and Peltigeraceae W. Watson are treated. Interesting species are: *Polychidium dendriscum* (Nyl.) Hensen new for continental Europe, *Pannaria tavaresii* P.M. Jørg. new for the peninsular Spain, and *Leptogium microphylloides* Nyl. and *Parmelia jamesii* Ahlner & P.M. Jørg., seldom mentioned from Spain. Additionnal 8 species are new for the flora of Galicia.

INTRODUCCION

Hemos reunido en este trabajo los liquenes con cianoficeas recogidos en la fraga de Caaveiro, La Coruña (N-O de España). La zona ha sido caracterizada en un trabajo anterior (Lopez de Silanes & Carballal 1987); añadiremos aquí que los materiales geológicos corresponden fundamentalmente a esquistos y granitos y las altitudes oscilan entre los 20 y 500 metros. La mayor parte del territorio estudiado está ocupado por un bosque perteneciente a la asociación *Blechno spicantis-Quercetum roboris* Tx. & Oberd. (1958).

Para cada especie indicamos su ecología y distribución para Europa, tomado esta última de Jørgensen (1978) y Clauzade & Roux (1985). Es de destacar el alto número de especies de distribución restringida, en su mayoría atlánticas o de tendencia oceánica y otras de distribución puntual, lo que da a la zona un gran interès floristico. En aquellas especies que son nuevas citas o están poco citadas

en España, así como en las que presentan características peculiares en cuanto a su morfología se efectua una breve descripción.

Las muestras se hallan en el herbario del Departamento de Biología Vegetal de la universidad de Santiago (SANT-Lich.) cuyo número de pliego se especifica. La recogida de material ha sido efectuada por el equipo de liquenólogos de dicho departamento.

CATALOGO

Collema flacidum (Ach.) Ach. - Encontrado en las grietas de un muro orientado al norte y en rocas a ras de suelo. Amplia distribución en Europa. 9m, esquistos, SANT-Lich. 2278.

Collema furfuraceum (Arn.) Du Rietz - Corticícola y muscícola-saxícola. Distribución: especie frecuente en lugares húmedos de Europa. *Castanea sativa*, SANT-Lich. 2261; 40m, *Fraxinus excelsior*, SANT-Lich. 2279; rocas graníticas con musgo, 90m, SANT-Lich. 2260.

Collema aff. ***nigrescens*** (Huds.) DC. - Nuestros ejemplares difieren de la descripción dada por Degelius (1954) en el grosor del talo, siendo de 120-130μm. El material ha sido revisado por el Dr. P.M. Jorgensen comunicandonos que pudieran ser ejemplares de esta especie especialmente gruesos. Sobre musgos en troncos de árboles. Distribución: en Europa de tendencia oceánica, en España de amplia distribución. *Castanea sativa*, SANT-Lich. 2283.

Ephebe lanata (L.) Vain. - Especie abundante y frecuente en las partes de la roca que están próximas al río o arroyos y en ciertas épocas pueden estar inundadas. Amplia distribución en Europa. 30m, esquistos, SANT-Lich. 2276.

Leptogium brebissonii Mont. (Syn.: *L. chloromelum* Mudd) - Corticícola y muscícola. Distribución: Europa atlántica y mediterránea. De España conocemos citas en Asturias (Vazquez & Crespo 1978), Mallorca (Font & Fiol 1985), Navarra (Etayo 1986), Guipúzcoa (B. Aguirre, com. pers.) y Cataluña (X. Llimona, com. pers.). Primera cita para Galicia. *Quercus robur*, SANT-Lich. 2249; *Castanea sativa*, SANT-Lich. 2285.

Leptogium aff. ***cochleatum*** (Dickson) P.M. Jorg. (Syn.: *L. tremelloides* (L. fil.) S.F. Gray, *L. azureum* auct. p.p.) - Nuestros ejemplares presentan un grosor del talo menor que el descrito por Jørgensen & James (1983). El Dr. P.M. Jørgensen al que le hemos enviado material lo considera conferible a dicha especie. Muscícola y corticícola. Distribución: regiones atlánticas de Europa. En España conocemos citas de Canarias (Follmann 1976) como *Leptogium azureum* (Swans.) Mont., de Navarra (Lacoizqueta 1885, Colmeiro 1889) y Lugo (Bellot 1952) como *Leptogium tremelloides* Fr., no sabemos con certeza si se trata de la misma especie al no poder estudiar los ejemplares de dicha citas. *Castanea sativa*, SANT-Lich 2289; *Fraxinus excelsior*, SANT-Lich, 2290.

Leptogium cyanescens (Rabenh.) Körber (Syn.: *L. caesium* (Ach.) Vain.) - En zonas húmedas, entremezclado con musgos, grietas de muros y directamente sobre la roca en fuentes donde la influencia del agua es directa. Especie oceánica

de amplia distribución en Europa. Esquistos, SANT-Lich. 2286; granito, SANT-Lich. 2288.

Leptogium hibernicum Mitchell ex Jørg. - Muscícola en troncos de árboles. Distribución: regiones atlánticas europeas. En España conocemos citas de Huesca (Llimona 1976), Salamanca (Marcos 1985) y de Guipúzcoa (B. Aguirre, com. pers.). Primera cita para Galicia. 90m, *Castanea sativa*, SANT-Lich. 2291; *Laurus nobilis*, SANT-Lich. 2292.

Leptogium liquenoides (L.) Zahlbr. (Syn.: *L. lacerum* (Retz.) S.F. Gray) - En rocas cubiertas de musgos y piedras de muros y suelos. Amplia distribución en Europa. Primera cita para Galicia. 90m, esquistos, SANT-Lich. 2293.

Leptogium microphylloides Nyl. - Talo marrón verdoso. Lóbulos alargados y estrechos no alcanzando los 0,5mm de ancho, casi siempre cubiertos de isidios granulosos o papilosos normalmente más estrechos en la base, de simples a ramificados, empiezan saliendo en el borde del lóbulo hasta llegar a ocultarlo. Siempre estéril. Nuestros ejemplares son pequeños, aproximadamente de 5mm de diámetro, sus talos aparecen aislados casi siempre en grietas de la corteza. La distribución que conocemos es la dada por Clauzade & Roux (1985) en el oeste, centro y sur de Francia. En España la cita Carballal & García-Molares (1988 b) en las cercanías de la ciudad de Pontevedra. *Fraxinus excelsior*, SANT-Lich. 2296.

Leptogium sinuatum (Huds.) Massal. (Syn.: *L. scotinum* (Ach.) Frey) - Muscícola en la parte vertical de un muro y en rocas a ras del suelo. Especie de amplia distribución en Europa. No conocemos citas de Galicia. Esquistos y granitos, SANT-Lich. 2294.

Leptogium tenuissimum (Dicks.) Körb. (Syn.: *L. sutile* (Schrad.) Torss.) - Saxícola-muscícola. Distribución: amplia en Europa. En España conocemos citas de Baleares (Maheu & Gillet 1921), Málaga (Seaward 1983) y de Cataluña (X. Llimona, com. pers.). Primera cita para Galicia. 90m, rocas graníticas, SANT-Lich. 2295.

Lobaria scrobiculata (Scop.) DC. - Corticícola, poco frecuente en la zona de estudio. Ampliamente distribuida por Europa. 250m, *Quercus robur*, SANT-Lich. 2297.

Nephroma laevigatum Ach. - Corticícola. Distribución: en Europa atlántico-mediterránea, muy extendida en España. 130m, *Quercus robur* y *Castanea sativa*, SANT-Lich. 2298.

Pannaria conoplea (Ach.) Bory - Muscícola-corticícola. Distribución amplia en Europa con tendencia atlántica; en España se limita su distribución al tercio norte. *Castanea sativa*, SANT-Lich. 2341.

Pannaria mediterranea C. Tav. - Corticícola y muscícola, a veces invade el talo de otros líquenes. Distribución: atlántico-mediterránea. *Castanea sativa*, SANT-Lich. 2329.

Pannaria rubiginosa (Ach.) Bory - Corticícola. Especie frecuente en la zona. Amplia distribución en Europa. *Quercus robur*, SANT-Lich. 2348; *Corylus avellana*, *Laurus nobilis*, *Castanea sativa*, SANT-Lich. 2346, 2347, 2349; *Fraxinus excelsior*, SANT-Lich. 2327.

Pannaria sampaiana C. Tav. - Corticícola. Un solo ejemplar de pequeñas dimensiones. Distribución: en Europa atlántica y mediterránea. Primera cita para Galicia. *Castanea sativa*, SANT-Lich. 2321.

Pannaria tavaresii P.M. Jørg. - Talo foliáceo en roseta, marrón claro o amarillento, P + naranja. Lóbulos ligeramente cóncavos con margenes que tienden a ser ascendentes y más pálidos. Isidios marginales simples o coraloides con frecuencia algo más ensanchados en el ápice. Especie corticícola encontrada en zonas sombrías del interior del bosque. Distribución: altántica y mediterránea en Europa. En España está citada de Canarias (Jøgensen 1978, Sanchez-Pinto & al. 1983, Hernandez-Padron 1985, Hernandez-Padron & al. 1987). Nuestra cita amplia su distribución al territorio de España peninsular. *Castanea sativa*, SANT-Lich. 2322.

Parmeliella jamesii Ahlner & P.M. Jørg. - Talo formado por pequeñas escuámulas ligeramente alargadas, 0,5-2mm de largo, más o menos continuas, de color gris azulado claro. Soralios granulosos difusos y marginales, pudiendo invadir la superficie del talo. Especie frecuente que puede confundirse con *Pannaria mediterranea* C. Tav. que es más abundante, cuando esta última presenta una coloración clara. Muscícola sobre troncos de árboles. Distribución: Europa atlántica. En España conocemos las citas de Canarias (Hernandez-Padron & al. 1987), Pontevedra (Carballal & Garcia-Molares 1988 a) y Guipúzcoa (B. Aguirre, com. pers.). *Corylus avellana*, *Ilex aquifolium*, SANT-Lich. 2323, 2333; *Castanea sativa* y *Eucalyptus globulus*, SANT-Lich. 2331, 2332.

Parmeliella plumbea (Lighlf.) Vain. - Corticícola, especie frecuente y la más abundante del género *Parmeliella*. Distribución: toda Europa con tendencia atlántica, menos frecuente en el centro. *Corylus avellana*, SANT-Lich. 2335; *Alnus glutinosa*, *Quercus robur*, SANT-Lich. 2338, 2336; *Castanea sativa*, SANT-Lich. 2334; *Fraxinus excelsior*, SANT-Lich. 2337.

Parmeliella testacea P. Jørg. - Corticícola y muscícola, frecuente sobre hepáticas foliosas. Distribución: Europa atlántica con algunos enclaves en el norte de Italia. Primera cita para Galicia. *Castanea sativa*, SANT-Lich. 2324; *Quercus robur*, SANT-Lich. 2342; *Fraxinus excelsior*, SANT-Lich, 2331.

Parmeliella triptophylla (Ach.) Müll. Arg. - Corticícola. Distribución: toda Europa excepto en la zona ártica. *Castanea sativa*, SANT-Lich. 2340.

Peltigera horizontalis (Huds.) Baumg. - Muscícola-saxícola. Distribución: amplia en Europa. No conocemos citas de Galicia. 40-400m, taludes, SANT-Lich. 2301.

Peltigera polydactyla (Necker) Hoffm. - Sobre restos vegetales, musgos y rocas. Distribución: amplia en Europa. 400m, granitos, SANT-Lich. 2300.

Peltigera praetexta (Flörk. ex Sommerf.) Zopf. - Es la especie de *Peltigera* más abundante y frecuente. Saxícola y muscícola. Distribución: casi toda Europa. 90m, rocas graníticas con musgo, SANT-Lich. 2303; 30-40m. talud rocoso, SANT-Lich. 2302.

Polychidium dendriscum (Nyl.) Hensen - Se diferencia de *P. muscicola* (Sw.) Gray en su talo de ramificación dicótoma que no presenta tomento y el ficobionte del género *Scytonema*. Corticícola. Distribución: Gran Bretaña, Irlanda y

Azores; No conocemos citas de Europa continental. *Castanea sativa*, SANT-Lich. 2304.

Sticta limbata (Sm.) Ach. - Corticícola y muscícola. Distribución: en Europa atlántico-mediterránea. *Corylus avellana, Castanea sativa, Quercus robur*, SANT-Lich. 2306, 2309, 2310; *Fraxinus excelsior, Eucalyptus globulus, Laurus nobilis*, SANT-Lich. 2305, 2307, 2308.

Sticta sylvatica (Huds.) Ach. - Muscícola y corticícola. Distribució: en Europa media y mediterránea con tendencia oceánica. De España conocemos citas de La Coruña (Colmeiro 1889, Crespo & al. 1981), Cataluña (X. Llimona, com. pers.), Navarra y Guipúzcoa (B. Aguirre, com. pers.). *Corylus avellana, Quercus robur, Castanea sativa*, SANT-Lich. 2311, 2318, 2316; *Alnus glutinosa, Laurus nobilis*, SANT-Lich. 2314, 2315; *Fraxinus excelsior* y *Eucalyptus globulus*, SANT-Lich. 2312, 2313.

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ÉTUDE COMPARÉE DE LA VÉGÉTATION BRYOPHYTIQUE DES TRONCS DE CHÊNE VERT ET DE CHÊNE PUBESCENT (PEUPLEMENTS ÂGÉS) DANS LA FORÊT DOMANIALE DE LA GARDIOLE DE RIANS (VAR, FRANCE)

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RÉSUMÉ - Étude de la végétation bryophytique des troncs de chêne vert et de chêne pubescent (âge: environ 61-66 ans en janvier 1984), sur deux niveaux de hauteur, dans la forêt domaniale de la Gardiole de Rians (Var, France). La surreprésentation des mousses (au moins 75% du total des taxons) par rapport aux hépatiques et la très grande pauvreté des communautés traduisent la xéricité du milieu ambiant, peu favorable aux épiphytes.

Les résultats des inventaires montrent qu'un seul ensemble de bryophytes, constitué d'un fond constant de trois taxons à large amplitude écologique, d'une hépatique xérophile et d'une mousse mésophile, occupe le niveau inférieur des troncs des deux espèces de chênes. Il en est de même pour les parties hautes où la communauté, constituée de plusieurs *Orthotrichum*, est très spécialisée (chêne vert: 62% de corticoles, chêne pubescent: 72,73%), mais demeure extrêmement fragmentaire sur *Quercus ilex*.

Enfin, quatre groupements (à *Frullania dilatata* et *Radula complanata* sur *Quercus ilex*, à *Homalothecium sericeum* et *Frullania dilatata* sur *Quercus pubescens*, à *Hypnum cupressiforme* var. *filiforme* ou à *Hypnum cupressiforme* var. *cupressiforme* sur les deux chênes) ont été décrits antérieurement pour la classe d'âge 6-31 ans. On peut déduire de la comparaison des données, que le vieillissement des phorophytes s'accompagne d'une diminution de la richesse des communautés, dont le recouvrement reste important.

ABSTRACT - A study of the bryophytic vegetation of holm-oak and pubescent oak trunks (age of stands: ca. 61-66 years in january 1984), on two height levels in the forest of La Gardiole de Rians (Var, France). The overrepresentation of mosses (at least 75% of the total number of taxa), compared to liverworts, and the very great poverty of the communities, express the dryness of the environment, which is unfavourable to epiphytes.

The results of the inventories show that a single unit of bryophytes, made of a constant set of three taxa with a wide ecological amplitude, a xerophilous hepatic and a mesophilous moss, occupies the lower level of trunks on both oak species. The same is true for the up-

per level whose community, constituted of several *Orthotrichum*, is very specialized (holm-oak: 62% of corticoles, pubescent oak: 72,3%), but remains fragmentary on *Quercus ilex*.

Finally, four groupings (*Frullania dilatata - Radula complanata* community on *Quercus ilex*, *Homalothecium sericeum - Frullania dilatata* community on *Quercus pubescens*, *Hypnum cupressiforme* var. *filiforme* or *Hypnum cupressiforme* var. *cupressiforme* ones on both tree species) have been distinguished for the lower level of trunks, according to the frequency and measured dominance of their components. The first three have been previously described for forests belonging to the 6-31 years age group. It can be deduced from the comparison of the data, that phorophyte ageing is accompanied by a decrease in the richness of the communities, whose cover remains important.

INTRODUCTION

Dans le cadre des activités du GRECO 130043 du C.N.R.S. "Ecologie des forêts méditerranéennes", des recherches pluridisciplinaires ont été entreprises sur plusieurs sites de basse Provence.

Elles comportent, entre autres, une analyse typologique des formations végétales qui correspondent aux différentes étapes de maturation forestière des écosystèmes, étude dans laquelle les bryophytes ont été prises en considération, compte tenu de leur importance en tant qu'indicateurs biologiques.

La forêt domaniale de la Gardiole, située entre Pourrières et Rians (Var) s'étend, sur environ 714ha, à l'intérieur d'une aire limitée du nord au sud et d'ouest en est par des points dont les coordonnées (en grades) sont les suivantes: 3,720 E x 48,415 N, 3,746 E x 48,395 N, 3,776 E x 48,429 N et 3,785 E x 48,401 N.

L'altitude varie de 380 à 630m et les affleurements géologiques, constitués de calcaires compacts, appartiennent au Jurassique supérieur.

Du point de vue climatique, par référence à la localité la plus proche (Pourrières, période 1951-1970), la moyenne annuelle atteint 746,7mm pour la pluviométrie (régime AHPE) et + 13,1°C pour la température.

Nos investigations n'ont concerné que des parcelles forestières correspondant à des taillis de *Quercus ilex* L. (*Quercetalia ilicis* Braun-Blanquet (1931) 1936) ou à des chênaies pubescentes (*Quercetalia pubescentis* Braun-Blanquet 1932) âgés d'environ 61-66 ans[1] en janvier 1984 (d'après Miglioretti 1983).

La localisation géographique des stations étudiées ici, dont la numérotation (tableaux 1 et 3) est identique à celle que nous avons utilisée dans deux contributions antérieures, n'a pas été rappelée.

Nous renvoyons donc le lecteur à ces travaux: Hébrard et Rolando (1985: 93, fig. 1, stations 16 à 20) pour les taillis de chêne vert et Hébrard (1987a: 115, fig. 1, stations 11 à 15) pour les chênaies pubescentes.

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(1) Ces limites d'âge sont évidemment approximatives et ne concernent que l'ensemble du peuplement arborescent de chaque station. Précisons que, pour des raisons matérielles, nous n'avons pas sondé chacun des arbres étudiés afin d'en connaître l'âge.

Dans chaque station, afin de disposer de données exhaustives sur la composition floristique des groupements bryophytiques de l'écorce, un inventaire détaillé a été effectué à deux niveaux de hauteur par rapport au sol (0-(46) 60cm et 42-(300) 700cm) sur les troncs (pente 90°) de 4 à 5 individus de chêne vert ou de chêne pubescent, dont la hauteur évaluée (*Quercus ilex:* 3 à 4,5m, *Quercus pubescens:* 5 à 7m) et la circonférence à la base correspondaient à la moyenne

	Taillis de chêne vert					Chênaies pubescentes					A	B
Numéros des stations	16	17	18	19	20	12	15	14	11	13		
Code des stations	2-143	1-153	2-153	1-153	4-263	4-63	3-263	2-263	3-63	1-263		
Altitude (m)	570	510	520	570	620	490	510	490	490	520		
Exposition de la station	N	W	ENE	N	N	N	N	NW	N	N		
Hauteur *Quercus ilex* ou *Q. pubescens* (évaluée en m)	4	4	4-4,5	3-3,5	3-4	5-6	6	6-7	6-7	8		
I. Bryophytes présentes depuis la base des troncs jusqu'à (hauteur en cm)	20-45	20-46	20-41	20-41	20-41	20-45	40-50	50-60	30-50	50-60		
Taxons à très large amplitude écologique												
Radula complanata	+	+	+	+	+	+	+	+	+	+	Co.Sax.	Circb.
Homalothecium sericeum		+	+	+	+		+	+	+	+	In.	Circb.
Hypnum cupressiforme var. *cupressiforme*	+	+	+		+	+	+		+	+	In.	Cosm.
Taxons xérophiles												
Frullania dilatata	+		+	+	+	+		+	+	+	Co.Sax.	Circb.
Zygodon baumgartneri					+			+	+	+	Co.Sax.	Sm.
Hypnum cupressiforme var. *strictifolium*				+	+	+					Co.Sax.	?
Leptodon smithii			+								Co.Sax.	Em.
Taxons mésophiles												
Hypnum cupressiforme var. *filiforme*	+		+	+		+	+	+	+	+	Co.Sax.	Circb.
Neckera complanata		+		+							Co.Sax.	Circb.
Orthotrichum affine var. *fastigiatum*	+								+		Co.	Circb.
Homalothecium lutescens										+	In.	Circb.
Orthotrichum striatum							+				Co.	Circb.
Nombre de taxons	5	4	6	6	6	5	5	5	7	7		
II. Bryophytes présentes plus haut (intervalles en cm)	46-300	47-300	42-200	42-300	42-200	46-600	51-400	61-700	51-600	61-500		
Taxons xérophiles												
Frullania dilatata	+	+	+	+	+	+	+	+	+	+	Co.Sax.	Circb.
Tortula laevipila var. *laevipila*					+		+	+		+	Co.	M.A.
Leucodon sciuroides								+		+	Co.Sax.	Scosm.
Orthotrichum diaphanum					+				+		Co.Sax.	Em.
Habrodon perpusillus					+						Co.	Sm.
Orthotrichum acuminatum										+	Co.	?
Orthotrichum tenellum								+			Co.	M.A.
Taxons mésophiles												
Orthotrichum affine var. *fastigiatum*		+			+		+	+	+	+	Co.	Circb.
Orthotrichum lyellii					+	+	+	+	+	+	Co.	Or.A.
Orthotrichum striatum				+	+		+		+	+	Co.	Circb.
Metzgeria furcata				+							Co.Sax.	Scosm.
Orthotrichum stramineum									+		Co.	Circb.
Ulota crispa									+		Co.	Circb.
Nombre de taxons	1	2	1	3	7	2	5	6	7	7		

Tableau 1 - Inventaire des bryophytes rencontrées sur les troncs (pente: 90°, 4 à 5 individus par station) de chêne vert et de chêne pubescent, depuis la base jusqu'à 2-7m au-dessus du sol, dans la forêt domaniale de la Gardiole de Rians (peuplements âgés d'environ 61-66 ans en janvier 1984). A: affinités selon le type de substrat, Co. = corticole, Co.Sax. = cortico-saxicole, In. = indifférent; B: distribution mondiale des taxons, Circb. = circumboréale, Cosm. = cosmopolite, Em. = euryméditerranéenne, M.A. = méditerranéenne - atlantique, Or.A. = oréoatlantique, Scosm. = subcosmopolite, Sm. = subméditerranéenne.

du peuplement. N'ont été envisagées, dans les conditions d'exposition globale de la station (chêne vert, N + NW + ENE: 80% des observations, W: 20%; chêne pubescent, N + NW: 100%), que les parties occupées par les bryophytes à l'exclusion de celles où dominent les lichens.

Enfin, la typologie des groupements muscinaux du niveau inférieur des troncs (jusqu'à 40-50cm au-dessus du sol), faisant intervenir la dominance des taxons, a été étudiée.

A cet effet, après avoir noté l'exposition de la surface choisie (entre 451 et 950cm^2, moyenne: 685,70 $\pm$ 151,27cm^2), on a mesuré le recouvrement de chaque bryophyte, en ramenant les aires à des figures géométriques simples (principalement rectangle et carré, plus rarement triangles).

STRUCTURE DE LA VÉGÉTATION BRYOPHYTIQUE DES ÉCORCES DE CHÊNE VERT ET DE CHÊNE PUBESCENT DANS LA FORÊT DOMANIALE DE LA GARDIOLE DE RIANS

(tableaux 1 et 2, figures 1, 2 et 3)

Nous avons volontairement limité cette étude aux chênaies âgées d'environ 61-66 ans à l'époque de nos travaux de terrain. En effet, le dépouillement des inventaires réalisés pour la classe d'âge 41-46 ans apporte peu de choses.

Toutefois, *Tortula virescens*, Pottiaceae non encore signalée dans le secteur, a été découvert sur l'écorce de jeunes *Quercus pubescens* (hauteur: 5-6m) dans la station 2-2284 (altitude: 460m, exposition: indéfinie), en compagnie des taxons suivants.

- Depuis le niveau du sol jusqu'à 40cm: *Bryum flaccidum, Frullania dilatata, Homalothecium lutescens, H. sericeum, Hypnum cupressiforme* var. *cupressiforme* et var. *strictifolium, Leucodon sciuroides, Orthotrichum acuminatum, O. affine* var. *fastigiatum, O. diaphanum, O. lyellii, O. striatum, O. tenellum, Tortula laevipila* var. *laevipila, T. princeps, T. virescens*.

- entre 40 et 100cm: *Frullania dilatata*.

Précisons enfin que les observations ont été effectuées dans des limites altitudinales peu différentes (maximum: 620m pour le chêne vert et 520m pour le chêne pubescent[1], minimum: 510 et 490m, moyenne: 548 et 500m).

Végétation bryophytique du niveau inférieur des troncs de chêne vert (0-46cm) et de chêne pubescent (0-60cm)

Dans les stations inventoriées, le peuplement muscinal propre au niveau inférieur des troncs a été observé depuis la surface du sol jusqu'à une hauteur maximale de 46cm sur chêne vert et 60cm sur chêne pubescent.

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(1) Par la suite, nous désignerons ces deux chênes par C.V. et C.P.

	Niveau inférieur						Niveau supérieur					
	C.V.		C.P.		C.V.+C.P.		C.V.		C.P.		C.V.+C.P.	
	n	%	n	%	n	%	n	%	n	%	n	%
Taxons												
Xérophiles	4	40,00	3	30,00	4	33,33	4	50,00	6	54,55	7	53,85
Mésophiles	3	30,00	4	40,00	5	41,67	4	50,00	5	45,45	6	46,15
A très large amplitude, vis-à vis de l'humidité	3	30,00	3	30,00	3	25,00	0	0	0	0	0	0
Total	10	100,00	10	100,00	12	100,00	8	100,00	11	100,00	13	100,00
Corticoles	1	10,00	2	20,00	2	16,67	5	62,50	8	72,73	9	69,23
Cortico-saxicoles	7	70,00	5	50,00	7	58,33	3	37,50	3	27,27	4	30,77
Indifférents	2	20,00	3	30,00	3	25,00	0	0	0	0	0	0
Aire de distribution mondiale des taxons : éléments												
Cosmopolite et subcosmopolite	1	10,00	1	10,00	1	8,33	1	12,50	1	9,09	2	15,38
Circumboréal	6	60,00	7	70,00	8	66,67	3	37,50	5	45,45	5	38,46
Euryméditerranéen	1	10,00	0	0	1	8,33	1	12,50	1	9,09	1	7,69
Subméditerranéen	1	10,00	1	10,00	1	8,33	1	12,50	0	0	1	7,69
Méditerranéen-atlantique	0	0	0	0	0	0	1	12,50	2	18,18	2	15,38
Oréo-atlantique	0	0	0	0	0	0	1	12,50	1	9,09	1	7,69
Autres	1	10,00	1	10,00	1	8,33	0	0	1	9,09	1	7,69
Mousses	8	80,00	8	80,00	10	83,33	6	75,00	10	90,91	11	84,62
Acrocarpes	2	25,00*	3	37,50*	3	30,00*	5	83,33*	9	90,00*	9	81,82*
Pleurocarpes	6	75,00*	5	62,50*	7	70,00*	1	16,67*	1	10,00*	2	18,18*
Hépatiques	2	20,00	2	20,00	2	16,67	2	25,00	1	9,09	2	15,38

Tableau 2 - Nombre et pourcentage de taxons de bryophytes rencontrés sur les troncs (niveaux inférieur et supérieur) dans les taillis de chêne vert (C.V.) et les peuplements de chêne pubescent (C.P.) âgés d'environ 61-66 ans en janvier 1984 (forêt domaniale de la Gardiole de Rians). Répartition selon les préférences écologiques (humidité, type de substrat) et l'appartenance aux aires de distribution mondiale; mousses acrocarpes, pleurocarpes, et hépatiques. *: en % du nombre total de mousses.

Néanmoins, dans toutes les yeuseraies considérées et dans deux chênaies pubescentes (stations 11 et 12), il ne s'étend souvent que jusqu'à 20 (30)cm sur beaucoup d'arbres.

Le tableau 2 fait apparaître de grandes analogies dans la structure du peuplement bryophytique épiphyte des deux *Quercus*.

On peut noter en particulier les faibles pourcentages de corticoles (10 à 20% du total de taxons), la forte proportion de muscinées à aire de distribution mondiale vaste (70 à 80%), notamment les circumboréales (C.V.: 60%, C.P.: 70%) et la rareté des méditerranéennes au sens large (C.V.: 20%, C.P.: 10%).

En outre, la prépondérance des mousses (80%) sur les hépatiques traduit bien la xéricité du milieu ambiant (bioclimat méditerranéen). Réciproquement, les différences sont discrètes. Tout au plus peut-on admettre que la représentation des xérophiles (C.V.: 40% du total de taxons, C.P.: 30%) et des cortico-saxicoles (C.V.: 70%, C.P.: 50%) est meilleure sur *Quercus ilex* qui colonise des biotopes plus secs et plus dégradés (affleurements rocheux importants).

D'autre part, le peuplement muscinal est très pauvre (nombre maximum de taxons par relevé, C.V.: 6, C.P.: 7, nombre minimum: 4 et 5, nombre moyen: 5,4 $\pm$ 0,80 et 5,8 $\pm$ 0,98).

Les proportions de bryophytes à fréquence très faible (F = 20% des relevés, C.V.: 30% du nombre total de taxons, C.P.: 40%) ou au contraire forte et très forte (F = 80-100% des relevés, C.V.: 40% du nombre total de taxons, C.P.: 50%) sont voisines pour les deux phorophytes (figure 1). Les secondes, un peu plus nombreuses, sont représentées essentiellement par trois ubiquistes *(Radula complanata, Homalothecim sericeum, Hypnum cupressiforme* var. *cupressiforme)* et une hépatique xérophile (*Frullania dilatata)*, auxquels s'adjoint *Hypnum cupressiforme* var. *filiforme* (mésophile), constant sur chêne pubescent (F = 60% des relevés en C.V. et 100% en C.P.).

Enfin, le nombre de familles de bryophytes est très réduit (C.V.: 6, C.P.: 5) et leur richesse en taxons diffère peu d'un chêne à l'autre (figure 3A).

Végétation bryophytique du niveau supérieur des troncs de chêne vert (42-300cm) et de chêne pubescent (46-700cm)

Sur les deux *Quercus* (tableau 2), les pourcentages de xérophiles (50% et 54,55% du nombre total de taxons) et de mésophiles (50% et 45,45%) sont proches, alors que les muscinées à large amplitude écologique et les indifférentes au type de substrat font défaut.

En ce qui concerne les xérophiles et les mésophiles, ces résultats peuvent s'expliquer du fait des caractéristiques du substrat et du milieu ambiant (compensation): écorce retenant moins bien l'eau, mais éclairement plus réduit (feuillage persistant en hiver) dans le cas de *Quercus ilex* et au contraire écorce plus riche en eau mais éclairement intense des parties moyennes et hautes des troncs en hiver et au printemps, dans le cas de *Quercus pubescens*.

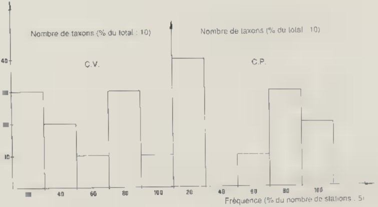

Fig. 1. NIVEAU INFERIEUR DES TRONCS

Figure 1 - Histogrammes des fréquences des bryophytes rencontrées sur le niveau inférieur des troncs de chêne vert (C.V.) et de chêne pubescent (C.P.) dans la forêt domaniale de la Gardiole de Rians (inventaire portant sur 4 à 5 individus par station).

De même, la représentation des cortico-saxicoles (37,50% et 27,27%), des éléments à vaste aire de distribution mondiale (50% et 54,54%, circumboréales: 37,50% et 45,45%), des méditerranéennes au sens large (euryméditerranéennes + subméditerranéennes + méditerranéennes - atlantiques, C.V.: 37,50%, C.P.: 27,27%) et des mousses (C.V.: 75%, C.P.: 90,91%) par rapport aux hépatiques sont très comparables.

Toutefois, les écorces lisses du chêne vert semblent un peu moins propices que celles du chêne pubescent, épaisses et crevassées, à l'installation des corticoles strictes (C.V.: 62,50% du total de taxons, C.P.: 72,73%). D'ailleurs, la richesse en bryophytes est plus grande avec *Quercus pubescens*, notamment si l'on compare les nombres moyens par relevé (C.V.: 2,8 ± 2,23, C.P.: 5,4 ± 1,85).

Le peuplement est aussi mieux structuré sur cet arbre (figure 2) puisque, par rapport à ce que l'on note pour le chêne vert, les taxons à fréquence très faible et faible (20-40% des relevés) ont une importance plus réduite (C.V.: 87,50% du nombre total de taxons, C.P.: 54,4%), contrairement à ceux dont la fréquence est forte et très forte (80-100% des relevés, C.V.: 12,5% du nombre total des taxons, C.P.: 27,27%).

Mis à part l'hépatique cortico-saxicole et xérophile *Frullania dilatata*, qui est absolument constante sur les deux chênes, et même parfois seule présente sur le niveau supérieur des troncs de certaines yeuseraies (stations 16 et 18, tableau 1), le groupement est constitué de corticoles strictes comme *Orthotrichum lyellii* (F, C.V.: 20%, des relevés, C.P.: 100%), *O. affine* var. *fastigiatum* (F, C.V.: 40%, C.P.: 80%) et plus accessoirement *Orthotrichum striatum* (F, C.V.: 40%, C.P.: 60%) ou *Tortula laevipila* var. *laevipila* (F, C.V.: 20%, C.P.: 60%). Il n'est

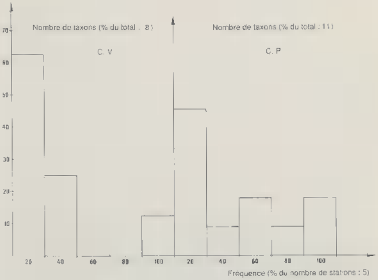

Fig. 2. NIVEAU SUPERIEUR DES TRONCS

Figure 2 - Histogrammes des fréquences des bryophytes rencontrées sur le niveau supérieur des troncs de chêne vert (C.V.) ou de chêne pubescent (C.P.) dans la forêt domaniale de la Gardiole de Rians (inventaire portant sur 4 à 5 individus par station).

donc parfaitement individualisé que sur *Quercus pubescens*. Parmi les espèces accidentelles, il convient de signaler *Ulota crispa*, rencontré une seule fois sur un gros chêne pubescent dans un ravin encaissé (station 11). Cette mousse, dont la présence indique une humidité atmosphérique élevée, du moins en dehors de la saison estivale, n'avait encore jamais été signalée en basse Provence.

Notons enfin (figure 3B) que le nombre de familles de bryophytes est faible (familles représentées par un seul taxon, C.V.: 4, C.P.: 3), celle des Orthotrichaceae regroupant le plus grand nombre de taxons, presque tous corticoles (C.V.: 4 taxons, C.P.: 8).

PRINCIPAUX GROUPEMENTS BRYOPHYTIQUES DU NIVEAU INFÉRIEUR DES TRONCS DE CHÊNE VERT ET DE CHÊNE PUBESCENT, ÉTABLIS D'APRES LA FRÉQUENCE ET LA DOMINANCE DE LEURS COMPOSANTES (tableau 3)

Hormis le groupement à *Hypnum cupressiforme* var. *cupressiforme*, les unités décrites dans un travail antérieur (Hébrard 1987b) pour des peuplements

d'arbres jeunes (6-31ans) de la forêt domaniale de la Gardiole de Rians, se retrouvent sous une forme appauvrie dans les chênaies plus âgées (61-66 ans).

Toutes s'intègrent aux *Leucodontetalia* (Von Hübschmann 1952) Lecointe 1975 et au *Frullania dilatatae* Lecointe 1975.

Groupement à *Frullania dilatata* et *Radula complanata*

Il n'a été rencontré que sur *Quercus ilex* (stations 19 et 20), en exposition N et NE.

Le recouvrement muscinal représente 45 et 60% de la surface de mesure. Ce groupement, avec seulement 3 taxons constants, est constitué par les xérophiles *Frullania dilatata* et *Hypnum cupressiforme* var. *strictifolium*, dominants par rapport à l'hépatique à vaste amplitude écologique *Radula complanata*.

Groupement à *Hypnum cupressiforme* var. *filiforme*

Il est fréquent sur les parties des troncs exposées au nord ou à l'est et son recouvrement atteint des valeurs plutôt élevées (38,95% à 88,55% de la surface de mesure, moyenne: 65,19 ± 17,79%). Toutefois, il est d'une grande pauvreté, avec

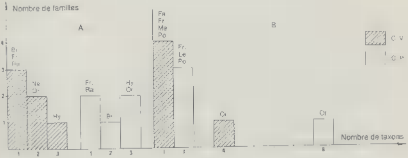

Fig. 3.

Figure 3 - Histogrammes de distribution du nombre de familles de bryophytes selon leur richesse en taxons présents sur les troncs de chêne vert (C.V.) et de chêne pubescent (C.P.) dans la forêt domaniale de la Gardiole de Rians (inventaire dans des peuplements forestiers âgés d'environ 61-66 ans en janvier 1984). A: niveau inférieur des troncs (C.V.: 0-46cm, C.P.: 0-60cm). B: niveau supérieur (C.V.: 42-300cm, C.P.: 46-700cm); Br. = Brachytheciaceae, Fa. = Fabroniaceae, Fr. = Frullaniaceae, Hy. = Hypnaceae, Le. = Leucodontaceae, Me. = Metzgeriaceae, Ne. = Neckeraceae, Or. = Orthotrichaceae, Po. = Pottiaceae, Ra. = Radulaceae.

Numéros des stations	19	20	16	18	14	12	17	15	11	13
Code des stations	3-153	4-263	2-143	2-153	2-263	4-63	1-153	3-263	3-63	1-263
Exposition (surface de mesure)	N	NE	NE	E	NW	N	NE	SE	W	SE
Intervalle de hauteur à partir du sol (cm)	0-41	0-41	0-45	0-41	0-50	0-45	0-46	0-50	0-49	0-40
Surface totale étudiée (cm2)	451	533	585	615	950	585	736	800	882	720
Recouvrement muscinal (% de la surface totale étudiée)	59,87	45,40	88,55	62,93	38,95	70,34	30,03	58,03	28,40	44,03
Différentielles des groupements										
Frullania dilatata	52,96	78,51	47,68	80,62	9,46	21,87	.	.	31,14	3,47
Radula complanata	0,37	3,31	10,42	0,78	0,27	2,31	69,23	.	17,96	.
Hypnum cupressiforme var. *filiforme*	.	.	41,89	18,60	90,27	75,82	.	.	.	.
Hypnum cupressiforme var. *cupressiforme*	.	.	.	.	.	.	3,62	98,87	50,30	.
Homalothecium sericeum	.	.	.	.	.	.	.	.	.	96,53
Autres taxons										
Hypnum cupressiforme var. *strictifolium*	46,67	18,18	.	.	.	.	.	.	.	.
Neckera complanata	.	.	.	.	.	.	27,15	.	.	.
Orthotrichum striatum	.	.	.	.	.	.	.	1,13	.	.
Orthotrichum affine var. *fastigiatum*	.	.	.	.	.	.	.	.	0,60	.

Tableau 3 - Groupements muscinaux du niveau inférieur des troncs de chêne vert et de chêne pubescent (peuplements âgés de 61-66 ans en janvier 1984) dans la forêt domaniale de la Gardiole de Rians. Pour chaque taxon, la dominance est exprimée en % de la surface totale occupée par les bryophytes.

seulement les constantes *Hypnum cupressiforme* var. *filiforme* (mésophile), *Frullania dilatata* et *Radula complanata*.

Sur chêne vert (stations 16 et 18), la seconde de ces muscinées, nettement xérophile, domine (D: 47,68% et 80,62% de la surface totale occupée par les bryophytes, contre 41,89% et 18,60% pour *Hypnum cupressiforme* var. *filiforme*), alors que l'inverse est constaté sur chêne pubescent (stations 14 et 12, D: 90,27% et 75,82% pour *Hypnum cupressiforme* var. *filiforme* contre 9,46% et 21,87% pour *Frullania dilatata*).

Groupements à *Hypnum cupressiforme* var. *cupressiforme* et à *Homalothecium sericeum* et *Frullania dilatata*

Ils remplacent les groupements précédents dans des biotopes plus xériques et notamment sur les parties basses des troncs de *Quercus pubescens* exposées au sud et à l'ouest. Tous deux sont floristiquement très pauvres (2 à 4 taxons par relevé).

Le premier (recouvrement muscinal: 28,40% à 58,03% de la surface de mesure) est caractérisé par la dominance de l'ubiquiste *Hypnum cupressiforme* var. *cupressiforme* dont la valeur, plutôt faible sur *Quercus ilex* (D: 3,62%, station 17), est au contraire considérable sur *Quercus pubescens* (D: 50, 30% et 98,87%, stations 11 et 15).

Enfin, le second groupement, rencontré sur *Quercus pubescens*, est presque entièrement constitué de colonies denses d' *Homalothecium sericeum* (D: 96,53% et recouvrement muscinal: 44,03% de la surface de mesure).

CONCLUSION

Des prospections effectuées dans les taillis de *Quercus ilex* et des forêts de *Quercus pubescens* âgées d'environ 61-66 ans (janvier 1984) sur le site de la Gardiole de Rians (Var) ont permis d'étudier, sur deux niveaux de hauteur par rapport au sol, la structure de la végétation bryophytique peuplant les troncs de ces chênes. L'inventaire approfondi des muscinées épiphytes a été réalisé en 10 stations (4 à 5 arbres par station).

Les résultats obtenus montrent que, pour le niveau inférieur (46 à 60cm au-dessus du sol), le peuplement bryophytique est pratiquement identique sur les deux phorophytes.

D'une grande pauvreté (total, C.V. ou C.P.: 10 taxons, C.V. + C.P.: 12), il est caractérisé fidèlement par *Radula complanata*, *Homalothecium sericeum*, *Hypnum cupressiforme* var. *cupressiforme*, à large amplitude écologique, accompagnés par *Frullania dilatata* (xérophile) et *Hypnum cupressiforme* var. *filiforme* (mésophile), ce dernier plus constant avec le chêne pubescent.

En ce qui concerne le niveau supérieur (entre 42 et 300-700cm au-dessus du sol), le peuplement muscinal n'est bien individualisé que sur *Quercus pubescens*

(total, C.V.: 8 taxons, C.P.: 11, C.V. + C.P.: 13), dont l'écorce rugueuse est plus favorable à l'installation des bryophytes.

Les muscinées les plus constantes sur ce chêne sont en particulier: *Orthotrichum lyellii, O. affine* var. *fastigiatum* (corticoles, mésophiles et photophiles) et *Frullania dilatata* (cortico-saxicole et xérophile), auxquels s'adjoignent *Tortula laevipila* var. *leavipila* (corticole et xérophile) et *Orthotrichum striatum* (corticole, mésophile et photophile).

D'autre part, dans une ambiance plutôt xérique (bioclimat méditerranéen, dégradation récente, C.V. + C.P.: 83,33% de mousses pour le niveau inférieur des troncs et 84,62% pour le niveau supérieur, xérophiles: 33,33% et 53,85%), des différences apparaissent lorsqu'on examine la structure de la végétation bryophytique des deux niveaux de hauteur, qui correspondent chacun à des conditions écologiques particulières (humidité et apport d'éléments minéraux provenant du sol plus importants, mais éclairement beaucoup plus faible pour les parties basses des troncs).

Ainsi, le peuplement du niveau supérieur est très spécialisé (C.V. + C.P., corticoles: 69,23% du nombre total de taxons, indifférentes au type de substrat: 0, contre 16,67% et 25% pour le niveau inférieur), puisque les Orthotrichaceae représentent 61,54% des taxons dénombrés pour l'ensemble C.V. + C.P. (25% pour le niveau inférieur).

En conséquence, les mousses acrocarpes (C.V. + C.P.: 81,82% du total des mousses) y sont bien représentées, alors qu'au contraire les Pleurocarpes, favorisées par la proximité du sol et indiquant une humification plus avancée du substrat, l'emportent largement sur le niveau inférieur des troncs (C.V. + C.P., Brachytheciaceae + Hypnaceae + Neckeraceae: 70% du total des mousses).

Enfin, l'analyse de relevés comportant la mesure précise de la dominance de chaque muscinée a permis de distinguer quatre groupements s'intégrant au *Frullanion dilatatae* Lecointe 1975 [*Leucodontetalia* (Von Hübschmann 1952) Lecointe 1975].

Mis à part le groupement à *Hypnum cupressiforme* var. *cupressiforme (Quercus ilex* et *Q. pubescens)*, les communautés à *Frullania dilatata* et *Radula complanata (Quercus ilex)*, à *Hypnum cupressiforme* var. *filiforme* (sur les deux chênes) et à *Homalothecium sericeum* et *Frullania dilatata (Quercus pubescens)*, très appauvries, mais dont le recouvrement est important, ont déjà été décrites pour la classe d'âge 6-31 ans (Hébrard 1987b).

Liste des bryophytes citées

Nomenclature conforme dans l'ensemble à Corley et al. (1982) et à Smith (1978) ou à l'Index Muscorum: taxons infraspécifiques, pour les mousses, ainsi qu'à Grolle (1983) pour les hépatiques.

Mousses. - *Bryum flaccidum* Brid., *Habrodon perpusillus* (De Not.) Lindb., *Homalothecium lutescens* (Hedw.) Robins., *Homalothecium sericeum* (Hedw.) B., S. et G., *Hypnum cupressiforme* Hedw. var. *cupressiforme*, *Hypnum cupressiforme* Hedw. var. *filiforme* Brid., *Hypnum cupressiforme* Hedw. var.

strictifolium Warnst., *Leptodon smithii* (Hedw.) Web. et Mohr, *Leucodon sciuroides* (Hedw.) Schwaegr., *Neckera complanata* (Hedw.) Hüb., *Orthotrichum acuminatum* Philib., *Orthotrichum affine* Brid. var. *fastigiatum* (Brid.) Hüb., *Orthotrichum lyellii* Hook. et Tayl., *Orthotrichum stramineum* Hornsch. ex Brid., *Orthotrichum striatum* Hedw., *Orthotrichum tenellum* Bruch ex Brid., *Tortula laevipila* (Brid.) Schwaegr. var. *laevipila*. *Tortula princeps* De Not., *Tortula virescens* (De Not.) De Not., *Ulota crispa* (Hedw.) Brid., *Zygodon baumgartneri* Malta.

Hépatiques. - *Frullania dilatata* (L.) Dum., *Metzgeria furcata* (L.) Dum., *Radula complanata* (L.) Dum.

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les gamétophytes et les sporophytes. Sous divers régimes lumineux, la morphologie des plastes est moins susceptible de changements chez les mousses que chez les plantes supérieures.

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Physiologie, Chimie

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Caractères physiol. des bryophytes polaires en relation avec les modes de distr. géogr., le climat polaire, et l'histoire de l'environ. des régions polaires. Plasticité phénotypique,

réponses opportunistes dans l'échange du CO_2 et la circulation de l'eau procurent aux bryophytes une tolérance considérable à la dessiccation et au froid.

89-269 NEHIRA K. - Germination of gemmae in some mosses collected from North America. *In:* Papers of Plant ecology and taxonomy to the memory of Dr Satoshi Nakanishi. The Kobe Geobotanical Society 1987: 355-360, 2 fig. (Dept. Biol., Fac. Integrat. Arts & Sci., Hiroshima Univ., Higashi-senda, Naka-ku, Hiroshima 730 Japan).

89-270 NEHIRA K. - Germination and protonemata. *In:* GLIME J.M., **Methods in bryology.** (Proc. Bryol. Meth. Workshop Mainz). Nichinan: Hattori Botanical Laboratory, 1988, pp. 113-117, 2 fig. (Ibidem).

89-271 RYDIN H. - Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* 1985, 45(3): 374-379, 1 tabl., 4 fig. (Inst. Ecol. Bot., Univ. Uppsala, Box 559, S-751 22 Uppsala).

Mesure de la quantité d'eau contenue dans le capitulum des sphaignes pour suivre la dessiccation pendant les périodes de climat sec et de basses eaux. Variation d'une esp. à l'autre. Influence de la présence de certaines esp. pour freiner la dessiccation des esp. voisines.

Répartition, Ecologie, Sociologie

89-272 BOCH M.S., KUZMINA E.O. - On *Sphagnum* mosses from the North-West of the RSFSR. *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(10): 1337-1346, en russe (Bot. Inst. V.L. Komarov ANSSSR, Leningrad, USSR).

89-273 CANALIS V. & CASAS C. - Novetas per a la brioflora dels Pirineus centrals. *Collect. Bot. (Barcelona)* 1985, 16(1): 59-61 (Dept. Bot., Fac. Biol., Univ. Barcelona, E-08028 Barcelona).

Liste de 10 esp. de mousses du Val d'Aran et d'Alta Ribagorça dont cert. sont nouv. pour la Catalogne.

89-274 DIA M.G., MICELI G. e NOT R. - Check-list delle Epatiche note in Sicilia. *Webbia* 1985, 39(1): 163-177 (Inst. & Orto Bot. dell'Univ., via Archirafi 38, I-90123 Palermo).

Liste de 107 hépatiques récoltés en Sicile (d'après la littérature et les récoltes récentes).

89-275 DOLL R. - Verbreitung und soziologisches Verhalten von *Orthotrichum lineare* Schwaegr. im Norden der DDR. *Gleditschia* 1985, 13(1): 141-145, 2 tabl., 1 carte (1020 Berlin, Rochstr. 9, DDR).

89-276 FRAHM J.P. (en coll. avec LAMY D., SCHUMACKER R., PHILIPPI G., RASTETTER V.) - La bryoflore des Vosges et des zones limitrophes. Duisburg: Universität-Gesamthochschule. 1989. Non paginé, 680 cartes. (Univ. Duisburg, Fachber. 6, Bot., Postfach 101503, D-4100 Duisburg).

Remarques générales, écol. des bryophytes de la région étudiée: Vosges cristallines et région du grès bigarré, region des collines, plaines du Rhin, Sundgau. Liste des bryophytes avec loc. d'après la littérature et des récoltes récentes de Frahm, Philippi, Rastetter ... Chaque taxon est cartographié pour les Vosges.

89-277 GEISSLER P. und BISANG I. - *Frullania inflata* Gott., ein neues thermophiles Element der Schweizer Moosflora. *Saussurea* 1985, 16: 95-100, 3 fig. (Conserv. & Jard. Bot., C.P. 60, CH-1292 Chambésy GE).

Descr. de la loc. (Tessin méridional) où a été trouvé *Frullania inflata* pour la 4° fois en Europe.

89-278 GUERRA J. y PUCHE F. - *Bryum dunense* Smith & Whitehouse en la Peninsula iberica y Baleares. Observaciones taxonomicas, corologicas y fitosociologicas. *Acta Bot. Malacitana* 1984, 9: 85-92, 2 tabl., 1 pl., 1 fig., 1 carte.

89-279 HÉBRARD J.P. et ROLANDO C. - Etude comparée du peuplement bryophytique de taillis de chêne vert d'âge différent en forêt domaniale de la Gardiole de Rians (Var,

France). *Ecol. Medit.* 1985, 11(2/3): 87-110, 14 tabl. (Lab. Bot. & Ecol. Médit., Fac. Sci. & Techn. St Jérôme, av. de l'Escadrille Normandie-Niemen, F-13397 Marseille Cedex 13).

Forte proportion de mousses photoxérophiles, de saxicoles, d'esp. de l'étage mésomédit., de cosmopolites et de circumboréales dans les taillis de chêne vert d'âge différent en forêt domaniale de la Gardiole de Rians. Influence de l'exposition des stations sur la composition spécifique. Effet litière et xéricité des microclimats limitent les possiblités d'implantation des bryophytes. Seules 2 mousses à très large amplitude sont à la fois constantes et dominantes: *Homalothecium sericeum* et *Hypnum cupressiforme* var. *cupressiforme*.

89-280 **KHMELJEV K.F., POPOVA N.N. - Rare species of bryophytes in the Voronezh Region.** *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(9): 1208-1214, 1 fig., en russe.

89-281 **MARSTALLER R. - Die Moosgesellschaften der Ordnung *Orthotrichetalia* Hadac in Klika et Hadac 1944. 19. Beitrag zur Moosvegetation Thüringens.** *Gleditschia* 1985, 13(2): 311-355, 10 fig., 13 tabl. (Sekt. Biol., Friedrich-Schiller-Univ., WB Ökol., 6900 Jena, DDR).

Structure, composition floristique, des 11 associations de l' *Orthotrichetalia* en Thuringe; influence de la pollution; discussion synsystématique. Nouvelle révision de la classe *Frullanio dilatatae-Leucodontetea sciuroidis* Mohan 1978 en Europe.

89-282 **MIHAI Gh., KAPTANIS E. - Some bryophytes of Lesbos (Greece).** *Analele Stiint. Univ. Al. I. Cuza Iasi, Sect. II a. Biol.* (ser. noua), 1984, 30: 55-57.

89-283 **NESCHATEYEV V. Yu. - Some associations of paludified pine forests in Leningrad region.** *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(10): 1362-1373, 1 fig., 1 tabl., en russe.

Bryophytes et lichens associés.

89-284 **OCHYRA R. and BARYLA J. - Wyginiecie Skorpionowca oblego *Scorpidium turgescens* (Musci) w Polsce. (Extinction of the turgid-feather-moss *Scorpidium turgescens* (Musci) in Poland.** *Chronmy Przyrade Ojczysta* 1988, 44(3): 68-69, 3 fig., en polon. (Dept. Bryol. Lichenol., Inst. Bot., Pol. Acad. Sci., Lubicz 46, 31-512 Krakow, Poland).

89-285 **OVSTEDAL D.O. - The vegetation of Lindas and Austrheim, western Norway.** *Phytocoenologia* 1985, 13(3): 323-449, 4 fig., 42 tabl. (Bot. Inst., P.O. Box 12, N-5014 Bergen).

Descr. des communautés végétales dans les cantons de Lindas et d'Austrheim. Descr. de nouv. ass. et sous-ass. Bryophytes et lichens associés.

89-286 **OTNYUKOVA T.N. - Ecology of some moss species of above-soil cover in the forests of Muisk Kettle (Bam Zone).** *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(10): 1373-1380, 3 fig., 2 tabl., en russe (Bot. Inst. V.L. Komarova ANSSSR, Prof. Popof Str. 2, Leningrad P-22, USSR).

89-287 **OTNYUKOVA T.N. - The ecology and phytocoenology of some moss synusia in the forests of the Muiskaya hollow (Baikal-Amur railway region).** *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(11): 1465-1476, 6 tabl., en russe, rés. angl. (Ibidem).

Structure et dynamique des synusies à *Rhytidium rugosum, Ptilidium ciliare, Pleurozium schreberi, Aulacomnium turgidum, A. palustre* et *Tomenthypnum nitens* dans 6 types de forêts de la région du train de Baikal-Amur.

89-288 **PEÑUELAS J., CANALÍS V. & CASAS C. - Aportació al coneixement de la brioflora aquàtica de l'alta muntanya pirinenca.** *Collect. Bot. (Barcelona)* 1985, 16(1): 51-57 (Dept. Ecol., Fac. Biol., Univ. Barcelona, E-08028 Barcelona).

Bryophytes aquatiques des Pyrénées centrales et orientales, au-dessus de 1600m, avec hab. Adaptation à l'environnement.

89-289 **ROSSELLÓ J.A. - Notes sobre la Brioflora Balear III.** *Collect. Bot. (Barcelona)* 1985, 16(1): 63-66, 2 fig. (Dept. Bot., Univ. Autonoma, Bellaterra, Barcelona, España).

Notes chorologiques de 16 bryophytes aux Baléares. *Athalamia hyalina*, *A. spathysii* et *Bryum alpinum* sont nouv. pour les Baléares.

89-290 **SCHOFIELD W.B. - Bryophyte disjunctions in the Northern Hemisphere: Europe and North America.** *Bot. J. Linn. Soc.* 1988, 98(3): 211-224, 8 fig. (Dept. Bot., Univ. Brit. Columbia, University Boulevard, Vancouver, B.C., V6T 2B1, Canada).

Disjonctions majeures des bryophytes: amphiatlantique et Europe W - Amérique NW. Relations avec les régimes climatiques. La connaissance du passé continental et de la biologie des bryophytes sont nécessaires pour une meilleure interprétation de ces disjonctions.

89-291 **SCOTT G.A.M. - Australasian bryogeography: fact, fallacy and fantasy.** *Bot. J. Linn. Soc.* 1988, 98(3): 203-210 (Queen's College, Univ. Melbourne, Parkville, Victoria 3052, Australia).

Les mécanismes possibles conduisant aux modèles actuels de distribution des bryophytes en Australasie ne peuvent être rigoureusement déduits des modèles eux-mêmes. Les données de distr. sont toutes imparfaites et changeantes. Causes possibles de disjonction. Imperfections de la théorie de l'endémisme.

89-292 **THEURILLAT J.P. et BEGUIN C. - Les groupements végétaux du canton de Neuchâtel (Jura, Suisse).** *Saussurea* 1985, 16: 67-93 (Cons. et Jard. Bot., C.P. 60, CH-1292 Chambésy GE).

Présentation systématique des groupements végétaux du canton de Neuchâtel. Validation de certaines unités. Bryophytes associés..

89-293 **WATTEZ J.R. et VAN HALUWYN Ch. - Contribution à l'étude de la végétation épiphytique (Lichens et Bryophytes) de la région guérandaise et des abords de l'estuaire de la Loire.** *Bull. Soc. Sci. Nat. Ouest France* n.s., 1985, 7(2): 70-93, 13 cartes, tabl. (Lab. Bot., Fac. Pharmacie, pl. Dewailly, F-80000 Amiens).

Les lichens et les bryophytes les plus intéressants (une dizaine) de la région guérandaise et des abords de l'estuaire de la Loire ont été cartographiés et font l'objet de commentaires sur leur rareté, leur répartitions géogr. et stationnelles. Noter la présence de *Lecanactis subabietina*. Descr. des principaux groupements de lichens épiphytes; influence de la pollution atmosphérique.

89-294 **WERNER J. - Vorkommen und Verbreitung der Grimmiales (Musci) im Grossherzogtum Luxemburg, im Westlichen Saarland und in einigen angränzenden Gegenden.** *Faun.-Florist. Notizen Saarland* 1985, 17(3): 355-376, 5 fig., 2 tabl. (32 rue Michel-Rodange, L-7248 Bereldange).

Liste de 24 Grimmiales avec loc. dans le Grand-Duché-de-Luxembourg et en Sarre occidentale. Phytogéogr. et écol. des Grimmiales; importance des facteurs géol. et pétrogr. dans cette distr. Liste des Grimmiales menacées.

89-295 **WERNER J. - *Lophozia turbinata* (Raddi) Steph. (Hepaticae) dans le sud-est du Grand-Duché de Luxembourg.** *Dumortiera* 1988, 42: 11-16 (Ibidem).

Descr. et ill. de *Lophozia turbinata* nouveau pour le Grand-Duché de Luxembourg. Ecologie et distr. en Europe.

Voir aussi: 89-252, 89-314, 89-317.

Pollution

89-296 **KISS T. - Regressive succession induced by acid rain in cryptogamic communities inhabiting *Juglans* bark.** *Symp. Biol. Hung.* 1987, 35: 865-882, 8 tabl., 4 fig. (Dept. Nat. Hist., Savaria Mus., Szombathely, Kisfaludy 9, 9701 Hungary).

Les corrélations significatives entre le pH de l'écorce et le SO_2 , entre le pH de la pluie et le SO_2 , entre le pH de l'écorce et le pH de la pluie reflètent des effets directs et indirects des polluants sur les plantes épiphytes et leurs substrats. Les thalles des lichens sont plus directement exposés et les plus touchés. Chez les mousses, sauf *Hypnum cupressiforme* , seuls les colonisateurs sont capables de survivre au stress.

89-297 **KWAPULINSKI J. and SAROSIEK J. - Radioecotoxicological influence of a power station on mosses.** *Symp. Biol. Hung.* 1987, 35: 815-826, 7 tabl., 1 fig. (Silesian Univ. Med., Dept. Toxicology, ul. Jagiellonska 4, 41200 Sosnowiec, Poland).
Etude de la variation du contenu en ^{226}Ra, ^{228}Ra et ^{137}Cs dans *Polytrichum commune* dans la région de Beskidy. L'influence de la minéralisation est directement et inversement proportionnelle à la précipitation annuelle sur la station. Relation avec la distance de la mousse par rapport à l'usine.

89-298 **MAKINEN A. - *Sphagnum* moss-bags in air pollution monitoring in the city of Helsinki.** *Symp. Biol. Hung.* 1987, 35: 755-776, 12 fig., 2 tabl. (Dept. Bot., Univ. Helsinki, Unioninkatu 44, SF-00170 Helsinki).
Sur la base de l'analyse atomique de l'absorption de *Sphagnum girgensohnii*, calcul et cartographie des valeurs mensuelles d'accumulation de Cd, Cr, Cu, Fe, Pb, Ni, V et Zn. 3 sources: traffic routier, usine thermique, incinération des ordures. La 1° est responsable du Fe, cendres, Pb, Cr, la 2° du Ni et du V, la 3° du Zn et du Cd.

89-299 **MAKINEN A. - Use of *Hylocomium splendens* for regional and local heavy metal monitoring around a coal-fired power plant in Southern Finland.** *Symp. Biol. Hung.* 1987, 35: 777-793, 5 fig., 3 tabl. (Ibidem).
Par spectroscopie atomique d'absorption, concentrations en Cd, Cr, Cu, Mn, Ni, Pb, V et Zn dans *Hylocomium splendens* récolté à proximité d'une usine électrique. Distr. des métaux dans la plante, relation avec la distance à l'usine.

89-300 **RON E., MAZIMPAKA V., VICENTE J. and GRANZOW DE LA CERDA I. - Urban bryophytes in spanish towns.** *Symp. Biol. Hung.*, 1987, 35: 727-753, 10 tabl., 4 fig. (Dept. Bot., Fac. Biol., Univ. Complutense, Madrid 3, Spain).
Présence.absence dans différents habitats, résistance aux conditions urbaines des bryophytes dans 4 villes du centre de l'Espagne.

89-301 **SAROSIEK J., WIEWIÓRKA Z. and MRÓZ L. - Bioindication of heavy metals toxicity of water by the liverwort *Ricciocarpus natans* (L.) Corda.** *Symp. Biol. Hung.* 1987, 35: 827-833, 3 tabl. (Dept. Ecol. & Nat. Prod., Inst. Bot., Wroclaw Univ., ul. Kanonina 6/8, 50-328 Wroclaw, Poland).
Etude des réactions symptomatiques de *Ricciocarpus natans* aux métaux lourds (Zn, Cu, Pb) pour l'utiliser comme indicateur biologique de pollution des eaux.

89-302 **SAROSIEK J. and SAMECKA-CYMERMAN A. - The bioindication of ethylene glycol in water by the mosses *Fontinalis antipyretica* L. and *Platyhypnidium rusciforme* (Neck.) Fleisch.** *Symp. Biol. Hung.* 1987, 35: 835-841, 2 tabl. (Ibidem).
Etude en laboratoire. *Fontinalis antipyretica* et *Platyhypnidium rusciforme* diffèrent dans leur vulnérabilité à l'action toxique du glycol éthylène. Les populations de ces mousses ont une susceptibilité écologique au glycol éthylène et sont capables de le décomposer.

89-303 **SAROSIEK J. and WIEWIÓRKA Z. - The electric properties of the aquatic moss *Fontinalis antipyretica* L. in the bioindication of environmental contamination by ethylene glycol.** *Symp. Biol. Hung.* 1987, 35: 843-848, 2 fig (Ibidem).

89-304 **SAROSIEK J., WOZAKOWSKA NATKANIEC H. and WIEWIÓRKA Z. - The effect of heavy metals on the dynamics of *Ricciocarpus natans* (L.) Corda population.** *Symp. Biol. Hung.* 1987, 35: 857-863, 3 tabl. (Ibidem).
Relations entre nombre de pieds de *Ricciocarpus natans* d'une population, la biomasse et les niveaux des contenus en métaux (V, Ni, Cr, Co) dans un environnement donné. Utilisation de *Riccioc. natans* comme biodincateur de la pollution des eaux par ces métaux.

89-305 **SÉRGIO C. - Epiphytic bryophytes and air quality in the Tejo Estuary.** *Symp. Biol. Hung.* 1987, 35: 795-314, 7 fig., 2 tabl. (Inst. Bot., Fac. Ci., 1294 Lisboa, Portugal).
Bryoflore épiphyte (32 taxons), principalement sur *Olea europea*, de 200 sites de l'estuaire du Tejo; présence, fertilité en fonction du SO_2. Noter la raréfaction et l'extinction de certaines espèces. Toxitolérance.dépaupérisation chez *Tortula laevipila*.

89-306 **WIEWIÓRKA Z. and SAROSIEK J. - The effects of non-ioning radiation on the aquatic liverwort *Ricciocarpus natans* (L.) Corda.** *Symp. Biol. Hung.* 1987, 35:

849-856, 2 tabl. (Dept. Ecol. & Natur. Prod., Inst. Bot., Wroclaw Univ., ul. Kanonina 618, 50-328, Wroclaw, Poland).

Voir aussi: 89-281.

Paléobryologie

89-307 BOSE M.N. and BANERJI J. - The fossil floras of Kachchh. I- Mesozoic megafossils. *Palaeobotanist* 1984, 33: 1-189, 71 fig., 55 pl.

Descr. de 44 genres dont 3 sont nouv. Les plantes du mésozoique du Kachchh peuvent appartenir au Jurassique moyen et supérieur. Descr. et ill. des taxons. Noter *Thallites* sp. et *Hepaticites sukhpurensis* sp. nov.

Bryophilie

89-308 DAVIDSON A.J. and LONGTON R.E. - Acceptability of mosses as food for a herbivore, the slug, ***Arion hortensis*****.** *Symp. Biol. Hung.* 1987, 35: 707-719, 5 tabl., 1 fig. (Dept. Bot., Univ. Reading, Whiteknights, Reading RG6 2AS, UK).

D'après le comportement de la limace, les auteurs suggèrent la présence de barrières chimiques et physiques empêchant la consommation des pieds de *Polytrichum commune* et de *Mnium hornum*.

89-309 DÖBBELER P. - Moosbewohnende Ascomyceten VII. Neufunde einiger Arten der Gattung ***Epibryon*****.** *Mitt. Bot. Staatssamml. München* 1985, 21(1): 757-773, 6 fig. (Inst. Syst. Bot., Univ. München, Menzingerstr. 67, D-8000 München 19).

Nouv. récoltes de 5 esp. communes d' *Epibryon* (Dothideales), ascomycètes bryophiles. Descr., ill. de certains caractères. Le genre *Thuidium* est un nouvel hôte pour *Epibryon diaphanum*, et *Pogonatum capillare* pour *E. pogonati-urnigeri*.

89-310 DÖBBELER P. und TRIEBEL D. - Hepaticole Vertreter der Gattungen ***Muellerella*** **und** ***Dactylospora*** **(Ascomycetes).** *Bot. Jahrb. Syst.* 1985, 107(1-4): 503-519, 4 fig., 2 tabl. (Ibidem).

Descr., ill. de quelques espèces hépaticoles des genres *Muellerella* et *Dactylospora* essentiellement lichénicoles: *M. frullaniae* sp. nov. et *M. rubescens* sp. nov. sur *Frullania*, *Dactylospora heimelii* (Zuka) c.n. (*Paryphydria*) sur Jungermanniales. Lichénisation non démontrée chez cette dernière esp.

89-311 DÖBBELER P., POELT J. und VEZDA A. - ***Lopadium hepaticola*** **spec. nov. ein moosparasitisches echtes** ***Lopadium*** **von der Südhalbkugel.** *Herzogia* 1985, 7(1-2): 81-91, 2 fig. (Ibidem).

Diagn., descr., ill. de *Lopadium hepaticola*, parasite d'hépatiques en Tasmanie. Clés aux genres séparés de *Lopadium* s. lat.

89-312 GERSON U. - Mites which feed on mosses. *Symp. Biol. Hung.* 1987, 35: 721-724 (Dept. Entomol., Fac. Agric., Hebrew Univ., Rehovot 76100, Israel).

89-313 ORTEGA A. y BUENDIA A.Ga. - Contribucion al estudio de la tribu ***Aleurieae*** **Seaver emend. Korf. en la Peninsula iberica.** *Cryptogamie, Mycol.* 1987, 8(2): 125-140, 26 fig. (Depto. Biol. Veg. (Bot.), Fac. Ci., Univ. Granada, Granada, España).

Etudes morphol. de 20 esp. d' *Aleurieae* Seaver emend. Korf (Pezizales) dont certaines sont bryicoles. Problèmes taxonomiques pour 7 autres.

Voir aussi: 89-325, 89-236.

Ouvrages généraux

89-314 ENGEL J.J. and HATTORI S. - Bryological contributions presented in Celebration of the distinguished Scholarship of Rudolph M. Schuster. *Beih. Nova Hedwigia* 1988, 90, 402 p. ill. (Dept. Bot., Field Mus. Nat. Hist., Roosvelt Road at Lake Shore Drive, Chicago, Ill 60605, USA).

6 contributions biogr., témoignage de ses élèves et amis, honorent R.M. Schuster (né en 1921) en tant qu'explorateur, enseignant et taxonomiste tout entier voué à la botanique et plus spécialement aux hépatiques. Les 23 contributions scientifiques reflètent le rôle éminent que tient R.M. Schuster en taxonomie et en systématique des hépatiques et aussi des mousses. Noter une bibliographie complète avec les dates effectives de publication. A l'occasion de ce jubilé, les espèces suivantes lui sont dédiées: *Fossombronia rudis* G.A.M. Scott et D.C. Pike d'Australie, *Frullania (Trachycolea) schusteri* Hattori de Queensland, *Plagiochila rudischusteri* Robinson du Venezuela, *Plagiochila rudolfii* Pocs de Tanzanie et *Fissidens schusteri* Iwats. et Wu de Chine.

89-315 MILLER N.G. - Bryophyte ultrastructure. *Advances Bryol.* 1988, 3: i-vii, 1-281, ill. (Biol. Surv., New York State Mus., Albany, NY 12230, USA). 6 contributions: cystosquelette, plastes, blépharoplaste, péristome, sporogenèse, jonction sporophyte-gamétophyte chez les bryophytes. Etat des connaissances, perpectives de recherches.

89-316 NEWTON M.E., WANSTALL P.J. and JURY S.L. - Bryology: modern research and the ways forward. *Bot. J. Linn. Soc.* 1988, 98(3): 183-275, ill. (Dept. Cell & Struct. Biol., Williamson Building, Univ. Manchester, Manchester M13 9PL, UK).

A l'occasion du bicentenaire de la Linnean Society of London, un meeting commun, Linnean Society et British Bryological Society a été organisé. 7 contributions furent présentées, exposant les approches contemporaines et les perspectives de recherches en taxonomie, cytologie, physiologie et distribution des bryophytes.

89-317 SCHUSTER R.M. - The Hepaticae of South Greenland. *Beih. Nova Hedwigia* "1988" 1989, 92: 1-255, 13 tabl., 27 fig. (Cryptog. Lab., Hadley, Massachusetts, USA).

Historique, paramètres biologiques, géologiques et climatiques du Groenland S. Reproduction, écologie, phytogéographie, dissémination des spores en environnement arctique. Problème taxonomique posé par les hépatiques arctiques. Traitement systématique des taxons avec loc., notes écol. et morphol.; clé aux esp. de certains genres. Bibliographie (5p.), index (3p.).

Documentation, Histoire des Sciences

Voir: 89-358.

Nouveau périodique. - ACTA BRYOLICHENOLOGICA ASIATICA

A new journal to report on short, original research findings on Asiatic bryophytes and lichens is scheduled to be published in January of 1990. The journal will appear twice a year, and be published in Chinese and English languages. All English articles shall have a Chinese abstract prepared by the author(s) or editor, and vice versa. Submission of manuscripts for the first issue shall be no later than August 30, this year. Manuscripts should be sent to the editor or the publisher at the following addresses: Dr. Benito C. Tan, c/o Cryptogam Herbarium, New York Botanical Garden, Bronx, NY 10458, USA; or Dr. Ming-Jou Lai, P.O. Box 190004, Taipei, Taiwan 24199. Subscription rate is about US$ 10.00 per year.

Cryptogamie, Bryol. Lichénol. 1989, 10 (3): 276-281

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Systématique, Nomenclature

89-318 ABASSI MAAF L., ROUX Cl. - *Hypocenomyce stoechadiana* nova lekenspecio (*Hypocenomyce stoechadiana* espèce nouvelle de lichen). *Bull. Soc. Linn. Provence* "1984" 1985, 36: 189-194, 2 fig., en espéranto. rés. franç. (Greco 43, Lab. Bot. & Ecol. Médit., Fac. Sci. & Techn. St Jérôme, Av. Escadrille Normandie-Niemen, F-13397 Marseille Cedex 13).

Diagn., descr., ill., chimie de *Hypocenomyce stoechadiana* esp. nouv. de Port-Cros (France).

89-319 AHTI T. - Correction to Proposal to conserve *Roccella* against *Thamnium* (lichenized fungi). *Taxon* 1985, 34(4): 709 (Dept. Bot., Univ. Helsinki, Unioninkatu 44, SF-00170 Helsinki).

Le type de *Roccella* est *Rocella fuciformis* (Linnaeus) A.P. de Candolle (*Lichen fuciformis* Linnaeus). (cf. *Taxon* 1984, 33: 330).

89-320 HAFELLNER J. - Studien über lichenicole Pilze und Flechten III. Die Gattung *Roselliniella* Vainio emend. Haf. (Ascomycotina, Dothideales). *Herzogia* 1985, 7(1-2): 145-162, 12 fig., 1 tabl. (Inst. Bot., Karl-Franzens-Univ. Graz, Holteigasse 6, A-8010 Graz).

Réinstallation de *Roselliniella* Vainio, distinct des genres *Adelococcus* Theiss. et Syd. et *Muellerella* Hepp ex Müll. Arg. - 4 esp. lichénicoles: *R. haplospora* (Th. Fr. et Almqv.) (= *Endococcus*), *R. frustulosae* (Vouaux) (= *Muellerella*), *R. kalbii* sp. nov. et *R. lopadii* (Vouaux) (= *Muellerella*). Clés aux esp. de *Roselliniella* et genres voisins. Descr., ill., taxonom., distr. de chaque taxon.

89-321 HAFELLNER J. - Studien über lichenicole Pilze und Flechten IV. Die auf *Brigantiaea* -Arten beobachteten Ascomyceten. *Herzogia* 1985, 7(1-2): 163-180, 4 fig. (Ibidem).

Clé, taxonom., descr., ill., distr. de 7 champignons lichénicoles sur *Brigantiaea* (Brigantiaeaceae, Lecanorales). Esp. nouv.: *Dactylospora frigida, D. porphyrea, Opegrapha brigantina, Buelliella pusilla.*

89-322 HERTEL H. und RAMBOLD G. - *Lecidea* sect. *Armeniaceae* : lecideoide Arten der Flechtengattungen *Lecanora* und *Tephromela* (Lecanorales). *Bot. Jahrb. Syst.* 1985, 107(1-4): 469-501, 3 tabl., 9 fig. (Bot. Staatssamml., Menzinger Str. 67, D-8000 München 19).

Lecidea sect. *Armeniaceae* (Th. Fr.) Ras. est divisé en deux entités selon les caractères des asques, des paraphyses, des conidiophores et des conidies: groupe *marginata* (membre des Lecanoraceae s.str.) et groupe *armeniaca* (membre des Tephroelataceae). Puisque des caractères adéquats n'ont pas été trouvés pour les séparer en genres distincts, les espèces du

groupe *marginata* sont classés sous *Lecidea* et celles du groupe *armeniaca* sous *Tephromela*. Nouv. comb.: *Lecanora albicans* (Nyl.) (*Lecidea*), *L. marginata* (Schaer.) (*Lecidea*), *Tephromela aglaea* (Sommerf.) (*Lecidea*), *T. armeniaca* (DC) (*Rhizocarpon*), *T. testaceoatra* (Vainio) (*Lecidea*) et *T. septentrionalis* sp. nov. du Groenland. Situation actuelle du genre *Lecidea*. Evaluation des caractères utilisés pour séparer les genres des lichens lécidéoides.

89-323 KASHIWADANI H. - Genus *Hyperphyscia* (Lichen) in Japan. *Bull. Natl. Sci. Mus. ser. B (Bot.)* 1985, 11(3): 91-94, 1 fig. (Dept. Bot., Natl. Sci. Mus., Tokyo, Japan).
Hyperphyscia crocata sp. nov. et *H. adglutinata* nouv. pour le Japon.

89-324 KUROKAWA S. - Studies on Australian and Tasmanian species of *Parmelia* (2). *Bull. Natl. Sci. Mus. ser. B (Bot.)* 1985, 11(3): 77-90, 11 fig. (Tsukuba Bot. Gard., Natl. Sci. Mus., Ibaraki, Japan).
Diagn., descr., ill., affinités de 10 *Parmelia* nouveaux: *P. adusta, P. capnoides, P. cerrussata, P. fumigata, P. interposita, P. lithophila, P. lithophiloides, P. murina, P. nana, P. pantherina*. - Nouvelles loc. en Australie pour *P. neoquintaria*. *P. pseudohypoleia* nouv. pour la Tasmanie.

89-325 MAYRHOFER H. und POELT J. - Die Flechtengattung *Microglaena* sensu Zahlbruckner in Europa. *Herzogia* 1985, 7(1-2): 13-79, 25 fig. (Inst. Bot., Karl-Franzens-Univ. Graz, Holteigasse 6, A-8010 Graz).
La révision du matériel européen des *Microglaena* sensu Zahlbruckner permet de distinguer 3 groupes d'espèces reconnus comme genres par les auteurs. *Chromatochlamys* Trev. (esp. type: *Chr. muscorum* (Fr.) c.n. (= *Verrucaria*), esp. se développant en parasite de mousses pleurocarpes, et 2 autres taxons: *Chr. larbaleshieri* (A.L. Smith) c.n. (= *Microglaena*), *Chr. vezdae* sp. nov.). *Protothelenella* Räsänen emend. Mayrh. et Poelt caractérisé, notamment par le phycobionte *Elliptochloris* (esp. type *P. reducta* (= *Microgl. sphinctrinoides* subsp. *reducta* , = *P. sphinctrinoidella* (Nyl.) c.n. (= *Verrucaria*) et 5 esp.: *P. corrosa* (Koerb.) c.n. (= *Limboria*), *P. leucothelia* (Nyl.) c.n. (= *Verrucaria*), *P. polytrichi* Dobb. et Mayrh. in Dobb. (sans phycobionte, parasite sur *Polytrichum sexangulare*), *P. sphinctrinoides* (Nyl.) c.n. (*Verrucaria*) et *P. xylina sp. nov.*). *Thelenella* Nyl. (syn. *Microglaena* Koerb.) (4 esp.: *T. justii* (Servit in Zschacke) c.n. (= *Microglaena*), *T. modesta* (Nyl.) Nyl., *T. pertusariella* (Nyl.) Vainio et *T. sampaiana* (B. de Lesd.) c.n. (= *Microgalena*)). Caractères morphol. et biol., distr. des taxons. Il est difficile d'établir les affinités de ces genres avec les familles d'Ascomycètes. *Protothelenella* appartient à la nouv. fam. des Protothelenellaceae.

89-326 POELT J. - *Rhizocarpon bryonthae* spec. nov. aus Grönland, eine parasitische Flechte auf der epibryen *Pertusaria bryontha*. *Herzogia* 1985, 7(1-2): 93-98, fig. (Inst. Bot., Karl-Franzens-Univ. Graz, Holteigasse 6, A-8010 Graz).
Diagn., descr., ill. de *Rhizocarpon bryonthae* sp. nov. du Groenland, parasite de *Pertusaria bryontha* bryicole. Clé aux *Rhizocarpon* croissant sur *Pertusaria*.

89-327 RUOSS E. - Die Renntierflechte *Cladonia stygia* in den Alpen. *Bot. Helvet.* 1985, 95(2): 239-245, 2 fig., 1 tabl. (Syst. Geobot. Inst. der Universität, Altenbergrain 21, CH-3013 Bern).
Taxonomie, écol., distr. de *Cladonia stygia* (Fr.) c.n. (= *C. rangiferina* f.) nouveau dans les Préalpes suisses. Comparaison avec *C. rangiferina* (L.) Web. L'auteur n'accepte pas la séparation des genres *Cladonia* et *Cladina*.

89-328 VITIKAINEN O. - Three new species of *Peltigera* (Lichenized Ascomycetes). *Ann. Bot. Fenn.* 1985, 22(4): 291-298, 6 fig. (Bot. Mus., Univ. Helsinki, Unioninkatu 44, SF-00170 Helsinki).
Diagn., descr., ill., affinités, distr. de *Peltigera kristinssonii* d'Islande, *P. pacifica* du Canada, et *P. retifoveata* de Finlande.

Voir aussi: 89-310, 89-311, 89-329, 89-341, 89-351, 89-352.

Morphologie, Anatomie

89-329 AHTI T. and HYVÖNEN S. - *Cladina stygia*, a common overlooked species of reinder lichen. *Ann. Bot. Fenn.* 1985, 22(3): 223-229, 2 fig. (Dept. Bot., Univ. Helsinki, Unioninkatu 44, SF-00170 Helsinki).

Taxonomie, descr., chimie, distr. de *Cladina stygia* caractérisé par la production de lames rouges dans les conidiomata et une forte mélanisation dans les tissus nécrotiques. Prés. d'atranorine et d'ac. fumarprotocétrarique dans cette esp. habitant les tourbières.

89-330 GARTNER G. - Die Gattung *Trebouxia* Puymaly (Chlorellales, Chlorophyceae). *Arch. Hydrobiol. Suppl.* 1985, 71(4): 495-548, 30 fig.

Cytomorphol., taxonom., systémat. des 25 esp. du genre *Trebouxia* (précédemment *Cystococcus* incluant *Pseudotrebouxia*) souvent phycobiontes de lichen.

89-331 GODEFROY A. - Rhizocarpons à thalle jaune dans la forêt de Fontainebleau. *Bull. Assoc. Franç. Lichénol.* 1985, 10(1): 15-20 (Lab. Biol. Végét., Route de la Tour Dénecourt, F-77300 Fontainebleau).

Descr. du thalle, des apothécies, des spores et ill. de *Rhizocarpon riparium* subsp. *lindsayanum*, *R. viridiatrum*, *R. lecanorinum* subsp. *lecanorinum* et subsp. *drepanodes*.

89-332 POELT J. - *Caloplaca epithallina*. Porträt einer parasitischen Flechte. *Bot. Jahrb. Syst.* 1985, 107(1-4): 457-468, 3 fig. (Inst. Bot., Holteigasse 6, A-8010 Graz).

Descr., variabilité, écol., distr. de *Caloplaca epithallina*, parasite strict sur un nombre d'hôtes taxonomiquement non liés mais bien définis parmi les Lecanorales.

89-333 TSCHERMAK-WOESS E. - *Elliptochloris bilobata* kein ganz seltener Phycobiont. *Herzogia* 1985, 7(1-2): 105-116, 2 fig. (Inst. Bot. & Bot. Gart., Univ. Wien, Rennweg 14, A-1030 Wien).

Descr. d' *Elliptochloris bilobata* phycobionte de *Catolechia wahlenbergii*, *Protothelenella corrosa*, *Pr. sphinctrinoides*, *Baeomyces rufus*. Relations avec le mycobionte, affinités systématiques.

Voir aussi: 89-318, 89-320, 89-321, 89-322, 89-323, 89-324, 89-325, 89-326, 89-328, 89-350, 89-351, 89-352, 89-353.

Cytologie, Ultrastructure

89-334 HOLOPAINEN T. and KÄRENLAMPI L. - Characteristic ultrastructural symptoms caused in lichens by experimental exposure to nitrogen compounds and fluorides. *Ann. Bot. Fenn.* 1985, 22(4): 333-342, 3 fig., 3 tabl. (Dept. Environm. Hygiene, Univ. Kuopio, P.O. Box 6, SF-70211 Kuopio).

Chez *Bryoria capillaris* et *Hypogymnia physodes*, les modifications ultrastructurales dues aux composés nitrogènes et fluorides sont différents de ceux dû à la fumigation de SO_2.

89-335 SCOTT M.G. and LARSON D.W. - The effect of winter field conditions on the distribution of two species of *Umbilicaria*. II. Fine structure and storage body distribution. *New Phytol.* 1986, 102(2): 313-326, 3 fig., 4 tabl. (Dept. Bot., Univ. Guelph, Guelph, Ontario , Canada NG6 2W1).

Effets de la transplantation sur l'ultrastructure et le mode de distr. des réserves de 2 lichens saxicoles: *Umbilicaria vellea* et *U. deusta*. Ce dernier peut accumuler des produits de photosynthèse pendant l'automne.

Physiologie, Chimie

89-336 CULBERSON C.F., CULBERSON W.L. and JOHNSON A. - Two new lichen products, elatinic acid and methylbarbatate, from the genus *Haematomma*

(Ascomycotina, Haematommataceae). *Mycologia* 1986, 78(6): 888-891, 1 tabl., 2 fig. (Dept. Bot., Duke Univ., Durham, North Carolina 27706, USA).

89-337 **FIEDLER P., GAMBARO V., GARBARINO J.A. and QUILHOT W. - Epiphorellic acids 1 and 2, two diaryl ethers from the lichen *Cornicularia epiphorella*.** *Phytochemistry* 1986, 25(2): 461-465, tabl. (Dept. Quimica, Fac. Ci., Univ. Frederico Santa Maria, Casilla 110-V, Valparaiso, Chile).

89-338 **HUNECKS S., TØNSBERG T. and BOLHMANN F. - (-)-Allo-pertusaric acid and (-)-dihydropertusaric acid from the lichen *Pertusaria albescens*.** *Phytochemistry* 1986, 25(2): 453-459, 2 fig., 2 tabl. (Inst. Pl. Biochem., Res. Dept. BioSci. & Med., Acad. Sci. GDR, Weinberg, 4010 Halle.Saale, East Germany).

Spectroscopie et chimie pour déterminer la nature de 2 acides carboxyliques lactone de *Pertusaria albescens* : acides (-)-allopertusarique et (-)-dihydropertusarique. Mise en évidence de taraxerone et d'une mixture de longues chaines d'alcools aliphatiques et d'acides gras chez *P. ophthalmiza*.

89-339 **INGOLFSDOTTIR K., HYLANDS P.J. and SOLBERG Y. - Structure of vesuvianic acid from *Stereocaulon* species** *Phytochemistry* 1986, 25(2): 550-553, 1 tabl. (Pharmacognosy Res. Lab., Dept. Pharmacy, Chelsea College, Univ. London, Manresa Road, London SW3 6LX, UK).

89-340 **LEUCKERT Ch. and MAYRHOFER H. - Chemische Flechtenanalysen IV.** *Herzogia* 1985, 7(1-2): 99-104, 3 fig. (Inst. Syst. Bot. & Pflanzengeogr., FU Berlin, Altensteinstrasse 6, D-1000 Berlin 3).

Présence de depside sulphurelline chez *Dimelaena australiensis*, d'atranorine, de chloroatranorine et de sulphurelline chez 6 specimens de *Lecanora sulphurella* (calycine en petites quantités dans l'un d'eux).

89-341 **MANRIQUE E., BALAGUER L., VALLANDARES F. - Sustancias liquenicas en táxones de la provincia de Madrid II. *Hypogymnia* gr. *intestiniformis*.** *Anales Jard. Bot. Madrid* 1985, 42(1): 81-85, 1 tabl. (Dept. Bot., Fac. Farm., Ciudad Univ., E-28040 Madrid).

La présence ou l'absence d'acide furmarprotocétrarique permet de distinguer *Hypogymnia atrofusca* d' *H. intestiniformis* s.str., qui ont respectivement 2 et 5 races chimiques.

89-342 **MAYRHOFER H. und LEUCKERT Ch. - Beiträge zur Chemie der Flechtengattung *Rinodina* (Ach.) Gray III.** *Herzogia* 1985, 7(1-2): 117-129, 1 tabl. (Inst. Bot., Karl-Franzens-Univ. Graz, Holteigasse 6, A-8010 Graz).

Chromatographie en couche mince de 52 spécimens de 26 espèces de *Rinodina*. Les acides confluentinique et 2'-O-méthylperlatolique sont nouv. chez *Rinodina*. Distinction de 2 races chimiques chez *R. subglaucescens*.

89-343 **PÉREZ URRIA E. and VICENTE C. - Regulation of urease by urea and its precursors in the lichen *Evernia prunastri*.** *Physiol. Pl. (Copenhagen)* 1985, 65(4): 433-438, 2 tabl., 6 fig. (Dept. Pl. Physiol., The Lichen Team, Fac. Biol., Complutense Univ., E-28040 Madrid).

89-344 **SCOTT M.G. and LARSON D.W. - The effect of winter field conditions on the distribution of two species of *Umbilicaria*. III. CO_2 exchange in thalli exposed to laboratory stimulations of winter.** *New Phytol.* 1986, 102(2): 327-343, 10 fig., 3 tabl. (Dept. Bot., Univ. Guelph, Guelph, Ontario, Canada N1G 2W1).

Umbilicaria vellea est exclu des habitats à neige parce qu'il est incapable de stocker les produits de photosynthèse sous la neige, contrairement à *U. deusta*.

89-345 **SIGAL L.L. and JOHNSTON J.W. Jr. - Effects of acidic rain and ozone on nitrogen fixation and photosynthesis in the lichen *Lobaria pulmonaria* (L.) Hoffm.** *Environm. Exper. Bot.* 1986, 26(1): 59-64, 2 fig., 1 tabl. (Environm. Sci. Div., Oak Ridge Natl. Lab., Oak Ridge, TN 37831, USA).

A pH 2,6, la pluie acide entraine une réduction de la fixation de l'azote et de la photosynthèse; pas de modification à pH 5,6-4,2. L'ozone n'a pas d'action significative,

mais il y a une tendance à une diminution de la fixation d'azote quant les concentrations d'O_3 augmentent. Pas d'interaction O_3 -pluie acide.

89-346 TAKALA K. and OLKKONEN H. - Titanium content of lichens in Finland. *Ann. Bot. Fenn.* 1985, 22(4): 299-305, 5 fig., 4 tabl. (Provincial Gouv. Kuopio, Hallituskatu 12-14, SF-70100 Kuopio).

Le contenu en Ti de lichens épiphytes et terricoles de 31 sites de Finlande dépend étroitement de l'espèce et varie selon différents facteurs (contenu en sulphure, pourcentage de dépôt de sulphate, poussières minéroorganiques de l'environnement).

Voir aussi: 89-318, 89-329, 89-335.

Répartition, Ecologie, Sociologie

89-347 ABASSI MAAF L., ROUX Cl. - Champignons lichénisés ou lichénicoles de la France méridionale: espèces nouvelles ou intéressantes (III). *Bull. Soc. Linn. Provence* "1984"1985, 36: 195-200 (Greco 43, Bot. & Ecol. Médit., Fac. Sci. & Techn. St Jérôme, Av. Escadrille Normandie-Niemen, F-13397 Marseille Cedex 13).

Liste de 32 lichens de la France méridionale avec notes dont *Agonimia octospora, Coccocarpia erythroxyli, Dimerella tavaresiana, Strangospora deplanata* et *Lecanora livido-cinerea* sont nouv. pour la France.

89-348 ANDREEVA E.I. - Lichenes epiphytici plantarum vascularium principalium regionis desertorum Kazachstaniae. *Bot. Mater. Gerbarija, Inst. Bot. Akad. Nauk Kazakstoj SSR* 1985, 14: 112-123, 2 tabl., en russe.

89-349 APTROOT A. und LUMBSCH H.T. - Ergänzungen zur Verbreitung von *Cladonia fragilissima*. *Herzogia* 1985, 7(1-2): 243-245 (Inst. Syst. Plantk., Heidelberglaan 2, NL-3508 TC Utrecht).

Cladonia fragilissima nouv. pour les Pays-Bas, et nouv. loc. en Rép. Féd. d'Allemagne.

89-350 BARRENO E. e RENOBALES G. - Aportaciones a la flora liquénica del País Vasco (España): rocas calcáreas, I. *Anales Jard. Bot. Madrid* 1985, 42(1): 61-80, 1 carte, 4 pl. (Dept. Bot., Fac. Farmacia, Univ. Complutense, E-28040 Madrid).

Liste de 21 taxons saxicoles des rochers calcaires du Pays basque espagnol. *Arthopyrenia saxicola, Encephalographa elisae, Gyalecta leucaspis, Lecanora agardhiana* subsp. *sapaudica, Opegrapha grumulosa, Petractis hypoleuca, Polyblastia deminuta, P. discrepans, P. amota, Staurothele catelepta, S. nantiana, S. rupifraga, Thelidium absconditum* et *T. minutulum* sont nouv. pour l'Espagne.

89-351 HERTEL H. - New or little-known New Zealand lecideoid-lichens. *Mitt. Bot. Staatssamml. München* 1985, 21(1): 301-337, 10 fig.

Carbonea phaeostoma, C. vorticosa, Fuscidea asbolodes, Lecidea endochlora, Poeltiaria corralensis, Porpidia arthrocarpa, P. macrocarpa, Rhizocarpon disporum, Rimularia insularis, Sporastatia testudinea sont nouv. pour la Nouvelle-Zélande et les îles subantarctiques. Nouv. loc. pour 14 autres lichens. Notes taxonom., morphol., répartition géographique; noter nouv. synonymes.

89-352 KASHIWADANI H. - Lichens of Dokgo Islands, the Oki Islands. *In:* **Natural History of the Hokuriku and San-in Districts (I).** *Mem. Natl. Sci. Mus.* 1985, 18: 95-106, 2 fig.

Liste des lichens des îles Dokgo et Oki, avec loc. Diagn., descr., ill. de *P. orientalis* sp. nov.

89-353 LARSON D.W., MATTHES-SEARS U. and NASH T.H. III - The ecology of *Ramalina menziesii* I. Geographical variation in form. *Canad. J. Bot.* 1985, 63(11): 2062-2068, 2 tabl., 6 fig. (Dept. Bot., Univ. Guelph, Guelph, Ontario, Canada N1G 2W1).

La morphologie de *Ramalina menziesii* est en relation avec la proximité de la côte et la latitude, la concentration en NaCl et la variation annuelle de la température, mais pas avec les plantes hôtes.

89-354 MAKRYI T.V. - **The epiphytic lichens of the Baikalsky mountain range.** *Bot. Zurn. (Moscow & Leningrad)* 1985, 70(11): 1441-1451, 2 tabl., en russe, rés. angl. (Central. Sibirsk. Bot. Sad SO, AN SSSR, Novosibirsk).
Liste de 92 esp. épiphytes, relations écologiques avec l'hôte.

89-355 OSORIO H.S. - **Contribution to the lichen flora of Uruguay. XXI. Additions to the Rio de la Plata lichen flora.** *Mycotaxon* 1985, 24: 463-466 (Dept. Bot., Mus. Nac. Hist. Nat., Casilla de Correo 399, Montevideo, Uruguay).
Liste de 21 lichens du Rio de la Plata avec hab. Noter l'habitat maritime pour *Lecidea icteria, Xanthoparmelia congensis* et *X. hypopsila.*

89-356 POELT J. und MAYRHOFER H. - **Die Flechtenflora der Modlinger Klause einst und jetzt (Niederösterreich).** *Ber. Deutsch. Bot. Ges.* 1985, 98(3-4): 385-392, 1 carte (Inst. Bot., Karl-Franzens-Univ. Graz, Holteigasse 6, A-8010 Graz).
La flore lichénique des rochers dolomitiques sur les 2 versants de Modlinger Klause a été étudiée pour la 1° fois en 1856-1857 et pour la 2° fois en 1984. Liste annotée des 82 esp. saxicoles, terricoles et bryicoles. Noter *Catillaria scotina* et *Dermatocarpon leptophyllum* nouveaux pour les Alpes.

89-357 VIVANT J. - **Les lichens des Pyrénées occidentales françaises et espagnoles.** *Doc. Ecol. Pyrén.* 1988, 5:3-119, 1 carte (16 rue Guanille, F-64300 Orthez).
804 lichens avec loc. dans les Pyrénées occidentales françaises et espagnoles dont nombreuses nouveautés pour les Pyrénées et pour la France.

Voir aussi: 89-283, 89-285, 89-293, 89-318, 89-322, 89-323, 89-324, 89-325, 89-326, 89-327, 89-328, 89-332.

Pollution

Voir: 89-226, 89-334, 89-345, 89-346.

Documentation, Histoire des Sciences

89-358 JOHNSON D.E. - **Literature on the history of botany and botanic gardens 1730-1840: A bibliography.** *Huntia* 1985, 6(1): 3-121 (Rancho Bernardo, 12283 Rouche House Road, San Diego, CA 92128, USA).

INFORMATIONS

Ouvrages récemment reçus

ENGEL J.J. and HATTORI S. - **Bryological contributions presented in celebration of the distinguished scholarship of Rudolf M. Schuster.** *BEIHEFTE ZUR NOVA HEDWIGIA* 1988, 90, 402p., ill. (ISBN 3-443-51012-4, Prix DM 280.-, Cramer, Berlin/Stuttgart).

FRAHM J.P. (en collaboration avec LAMY D., SCHUMACKER R., PHILIPPI G., RASTETTER V.) - **La bryoflore des Vosges et des zones limitrophes.** Duisburg: Universität-Gesamthochschule, 1989, non paginé, ill. (Chez l'auteur: Univ. Duisburg, Fachber. 6, Bot., Postfach 101503, D-4100 Duisburg).

MILLER N.G. - **Bryophyte ultrastructure.** *ADVANCES IN BRYOLOGY* 1988, 3, 281p., ill. (ISBN 3-443-52001-4, Prix DM 120.-, Cramer, Berlin/Stuttgart).

NEWTON M.E., WANSTALL P.J. and JURY S.L. - **Bryology: modern research and the ways forward.** *BOTANICAL JOURNAL OF THE LINNEAN SOCIETY* 1988, 98(3): 183-275, ill. (S.L. Jury, Dept. Bot., Univ. Reading, P.O. Box 221, Reading, RG6 2AS, UK).

SCHUSTER R.M. - **The Hepaticae of South Greenland.** *BEIHEFTE ZUR NOVA HEDWIGIA* "1988" 1989, 92, 255p., ill. (ISBN 3-443-51014-0, Prix DM 170.-, Cramer, Berlin/Stuttgart).

Congrès

3th International colloquium on Lichen Biology - Madrid- Spring 1990, organisé par l'International Association of Lichenology. Renseignements: C. Vicente, Lab. Plant Physiology, Fac. Biology, Complutense Univ., E-28040 Madrid).

Union Internationale des Instituts de Recherches forestières (IUFRO) - 15e Congrès mondial, Montréal, 5-11 août 1990. Renseignements: D.K. Lemkay, IUFRO Montréal 1990 Inc., C.P. 1990, Place d'Armes, Montréal, Canada H2Y 3L9.

Congress of East Asiatic Bryology - Helsinki, 12-19 août 1990 - Organisé par le Dept. Bot. (Univ. Helsinki) et la Finnish Bryological Society, à l'occasion du 350e anniversaire de l'Université d'Helsinki. Renseignements: T. Koponen, Dept. Bot., Univ. Helsinki, Unioninkatu 44, SF-00170 Helsinki.

International Symposium on Endangered Bryophytes in Europe: Causes and Conservation - Uppsala, 24-28 septembre 1990 - Organisé par le Swedish Committee for the conservation of endangered bryophytes. Renseignements: N. Cronberg, Dept. Systematic Botany, Univ. Lund, Ostra Vallg 18-20, S-22361 Lund.

Annonces de décès

Nous avons appris la mort de **A. NOGUCHI** survenue le 24 septembre 1988. Né en 1907, A. Noguchi était l'auteur de nombreux travaux bryologiques concernant les mousses asiatiques, et notamment de *Illustrated moss flora of Japan* dont les deux premiers fasc. sont parus et qui sera continuée par Z. Iwatsuki. Une notice avec photo est parue dans le *Proc. Bryol. Soc. Japan* 1989, 5(1), par S. Inoue, en japonais.

Nous avons appris la mort subite de **Stanley Wilson GREENE,** survenue le 14 juin 1989. Né le 19 juillet 1928, S.W. GREENE fut en 1969, parmi les membres fondateurs de l'International Association of Bryologists dont il était l'actuel Président. En 1980, il créa *'The Bryological Times'* qui, reflet de sa personnalité, plus qu'un simple journal de liaison, devint le lien très vivant (grâce à ses éditions européenne, américaine et asiatique) des bryologues du monde entier. S.W. GREENE s'est consacré aux mousses antarctiques, mais sa principale préoccupation fut de donner à ses collègues, débutants et confirmés, des outils documentaires spécifiques; ainsi, le *Conspectus of Bryological Taxonomic Literature* dont la première partie est parue en 1988 et la deuxième vient d'être publiée. Nous souhaitons, tous, que les données qu'il a patiemment réunies puissent, malgré sa disparition, être éditées. Nous sommes persuadés que ceci serait son voeu le plus cher.

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INSTRUCTIONS AUX AUTEURS

Les manuscrits proposés à CRYPTOGAMIE, Bryologie-Lichénologie, doivent être fournis en double exemplaire, dactylographiés à double interligne, sans rature ni surcharge, et comporter des marges droites et gauches de 25mm, et hautes et basses de 50mm. Les auteurs sont priés de fournir des textes d'excellente qualité d'encrage. Chaque manuscrit devra comporter:

- le titre de l'article, dans la langue du manuscrit, et sa traduction en anglais;
- le titre courant (haut-de-page) de 50 signes au maximum;
- le nom et les prénoms des auteurs et leurs adresses;
- deux résumés, l'un dans la langue du manuscrit, l'autre en français ou en anglais, d'environ 180 mots ou 15 lignes, faisant ressortir les résultats essentiels exposés dans l'article;
- des légendes explicites des figures, planches et tableaux, sur feuilles séparées;
- une liste bibliographique par ordre alphabétique des auteurs et chronologique par auteurs sans tenir compte des auteurs secondaires. Les titres des périodiques devront être abrégés suivant le B-P-H (Botanico-Periodicum-Huntianum, Pittsburg: Hunt Botanical Library, 1968), les ouvrages cités selon F.A. Stafleu & R.S. Cowan, 1976- ... Taxonomic literature. Ed. 2 Utrecht/Antwerpen: Bohn, Scheltema & Holkema (*Regnum vegetabile* 94, 98, 105, 110...).

MONTAGNE C., 1838 - Centurie des plantes cellulaires exotiques nouvelles; *Ann. Sci. Nat., Bot.*, 2, 9: 38-57.

NEES VON ESENBECK C.G., 1836 - Hepaticae. *In:* Lindley J., A natural system of Botany... Ed. 2. London. Pp. 412-414.

WATSON E.V., 1971 - The structure and life history of bryophytes. Ed. 3. London: Hutschinson University Library. 211 p., 26 fig.

TEXTE. - La présentation du texte devra faire apparaitre clairement ses subdivisions et leur hiérarchie ainsi que le début des paragraphes. Les noms des auteurs qui suivent les binômes latins devront être abrégés selon G. Sayre et al., 1964 *(The Bryologist* 67 (2): 113-135). Les renvois à la liste bibliographique se feront par le nom de l'auteur et l'année de publication (ex.: (Dubois 1980) ou Dubois (1980) et non par les renvois numériques. La place des illustrations devra être indiquée dans la marge. Les notes infrapaginales sont à éviter.

ILLUSTRATIONS. - Toutes les illustrations, y compris les tableaux, doivent être des originaux de qualité suffisante pour la reproduction directe en offset. Elles devront comporter les échelles et symboles nécessaires à leur compréhension. En particulier, les tableaux devront être dactylographiés par une machine électrique ou composés en lettres de transfert. Les positifs des documents photographiques devront être montés par planches. Toutes les illustrations doivent être numérotées dans l'ordre d'appel dans le texte. Les auteurs devront tenir compte du format de la revue (11 x 18cm) et de la réduction que subissent éventuellement les originaux en choisissant l'épaisseur des traits et la taille des lettres et des chiffres.

Les tirages à part et les planches photographiques sont à la charge des auteurs.

SOMMAIRE

Cryptogamie, Bryol. Lichénol., 1989, 10 (3): 189-282